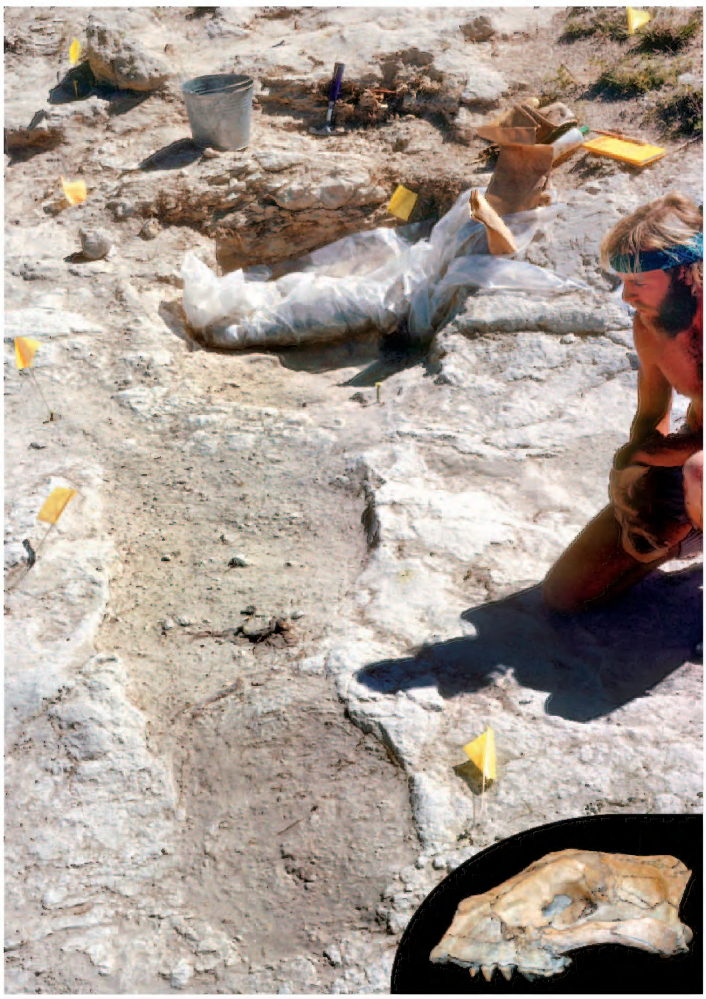
Evolution of Large Carnivores during the mid-Cenozoic of North America

The Temnocyonine Radiation (Mammalia, Amphicyonidae)

Robert M. Hunt, Jr.



Bulletin of the American Museum of Natural History

EVOLUTION OF LARGE CARNIVORES DURING THE MID-CENOZOIC OF NORTH AMERICA: THE TEMNOCYONINE RADIATION (MAMMALIA, AMPHICYONIDAE)

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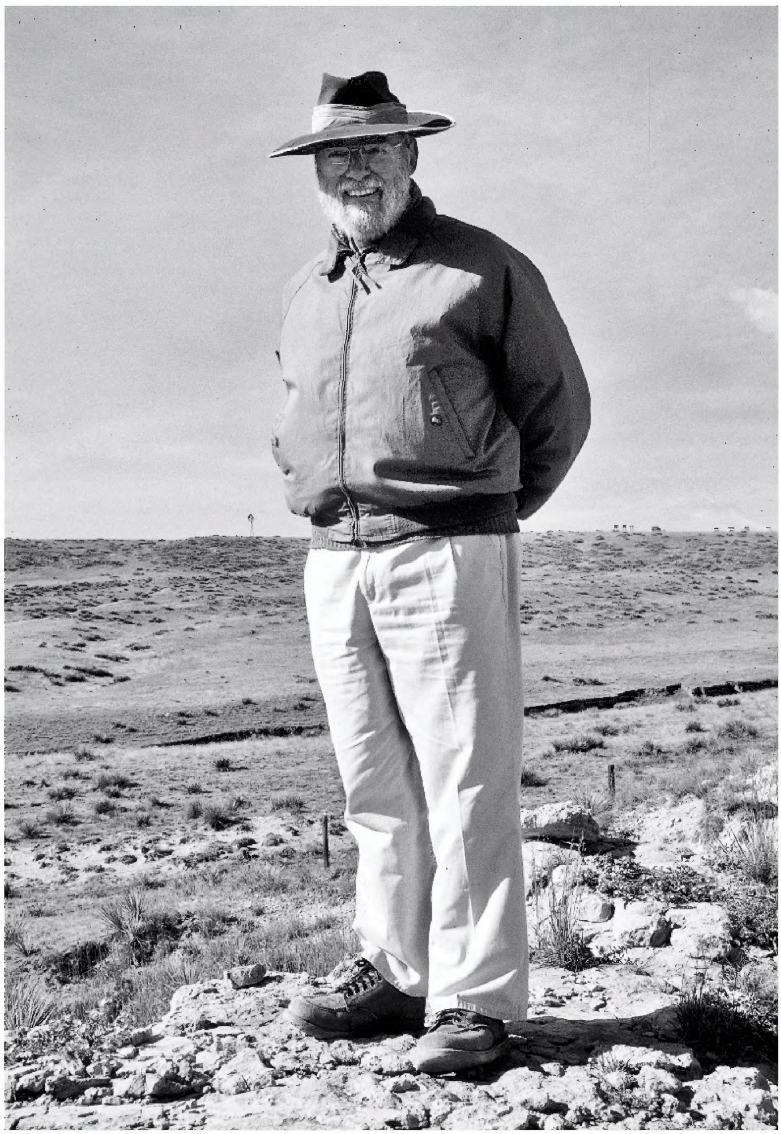

RICHARD H. TEDFORD

Pawnee Buttes, Colorado, 1999

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ABSTRACT

This study describes and summarizes the Temnocyoninae (Mammalia, Carnivora), a subfamily of amphicyonid carnivores of considerable diversity and singular ecomorphology within Cenozoic faunas of North America. In temnocyonines, we see the first carnivorans to occupy an ecological niche as large cursorial predators. The subfamily is confined to the Arikareean NALMA, ranging in age from the latest early Oligocene to the early Miocene. Distributed from the Pacific Northwest to the Great Plains and Florida, there are four genera (*Temnocyon*, *Mammacyon*, *Delotrochanter* n. gen., *Rudiocyon* n. gen.) and 12 species, of which eight are newly described (*Temnocyon subferox*, *T. fingeruti*, *T. macrogenys*; *Rudiocyon amplidens*; *Mammacyon ferocior*; *Delotrochanter petersoni*, *D. oryktes*, *D. major*). Among the specimens examined are eight skulls, three with intact basicranial morphology that establish the presence of a plesiomorphic arctoid auditory region in the subfamily. Temnocyonine dentitions and postcranial skeletons reveal a blend of morphological characteristics not previously nor subsequently seen among the Carnivora. From a stem species, *Temnocyon altigenis*, there evolve both large hypercarnivorous (*Temnocyon*) and durophagous forms (*Mammacyon*, *Delotrochanter*); these genera share a derived dentition that defines the Temnocyoninae. *Delotrochanter oryktes* n. sp., an early Miocene species, was found in a den, suggesting a possible burrowing capability and sheltering of offspring.

The John Day basin of Oregon and the central Great Plains (western Nebraska, southeast Wyoming) are the source of most temnocyonine fossils; a few have been found in southern California and Florida, indicative of a continent-wide distribution. Temnocyonines have often been confused with canids, however their basicranial anatomy places them securely within the Amphicyonidae. First discovered in the 1870s, only ~30 individuals comprise the entire record of the subfamily. Many were found in proximity to radioisotopically calibrated tuffs and ignimbrites and/or were closely associated with mammals of established biochronologic age. Thus, most species can be placed in a temporal context. With rare exception, the fossils represent isolated occurrences, hence estimates of variation within a population are lacking.

Cursorial postcranial features characterize several lineages (*Mammacyon*, *Delotrochanter*) and probably were present in other temnocyonines known only from dental remains. Late Oligocene *Mammacyon ferocior* and early Miocene *Delotrochanter oryktes* evolved uniquely configured crushing cheek teeth and cursorial limbs, combining distinctive dental and skeletal traits in a manner not seen in any living carnivore. These species are interpreted as large durophagous predators with craniodental characteristics that parallel living hyaenids (*Crocuta crocuta*) and postcranial adaptations approaching those of cursorial canids such as the wolf (*Canis lupus*). Expansion of semiarid grasslands and savanna during the late Oligocene and early Miocene in the central Great Plains seems to have favored the evolution of these wide-ranging durophagous amphicyonid carnivores.

Analysis of the jaws of temnocyonines employing Therrien's method of beam analysis demonstrates pronounced bending strength focused beneath the crushing dental battery in the molar region. Similarly, the canines and mandibular symphysis manifest an ability to resist strong parasagittal, transverse, and torsional forces occurring during prey capture and feeding.

Temnocyonines share a pronounced similarity in dentition with European haplocyonine beardogs, which doubtless are their sister group among the Amphicyonidae. Some haplocyonines also show cursorial tendencies. Examination of European material, however, reveals subtle dental distinctions indicating that the evolution of the two subfamilies proceeded separately yet in parallel in Europe and North America.

INTRODUCTION

In North America the guild of large mammalian carnivores was transformed at specific intervals during the Cenozoic. At these times, long-standing associations of large predators were disrupted by extinctions, resulting in loss of species diversity, and were replaced by species representing newly emergent endemic or immigrant taxonomic groups.

The transition from the Oligocene to the Miocene epoch is marked by such an event:

an archaic creodont-carnivoran association of hyaenodonts, nimravid cats, and endemic daphoenine amphicyonids is replaced by a new carnivoran association characterized by Eurasian migrant amphicyonines, hemicyonine ursids, and the first New World felids (Hunt, 2002a, 2004). The decline of the archaic association takes place over ~4–5 million years in the late Oligocene, from ~29 Ma to 24–25 Ma, and the new arrivals are not evident until ~23 Ma in the early Miocene. During this transitional interval there appears a unique and specialized group of amphicyonids, the Temnocyoninae, that diversified into 3–4 lineages over ~7 million years (~29–22 Ma). Temnocyonines are the only group of large North American carnivorans to successfully diversify at this time, filling an ecological vacuum that developed during the North American faunal turnover event at the Paleogene-Neogene boundary (fig. 1, NALCTE).

Temnocyonines are the first New World carnivorans to combine large body size, a digitigrade stance, and elongated limbs, with a uniquely configured crushing dentition. The subfamily represents a radiation yielding a number of cursorial durophagous species, the earliest experiment uniting these locomotor and feeding strategies within the Carnivora in North America. Their origin from a plesiomorphic amphicyonid stem is evidenced by basicranial morphology and a rudimentary auditory bulla structure.

Temnocyonine genera mark out three and possibly four lineages: *Temnocyon*, including the stem temnocyonine species, *T. altigenis*; *Mammacyon*, the first line to attain large size and to develop a massive crushing dentition; *Delotrochanter*, new genus, a second durophagous group reaching large size later in the Arikareean than *Mammacyon*; and *Rudiocyon*, new genus, exclusive to the John Day Formation of Oregon and a possible relative of *Mammacyon*, distinguished by the proportions of its molar teeth.

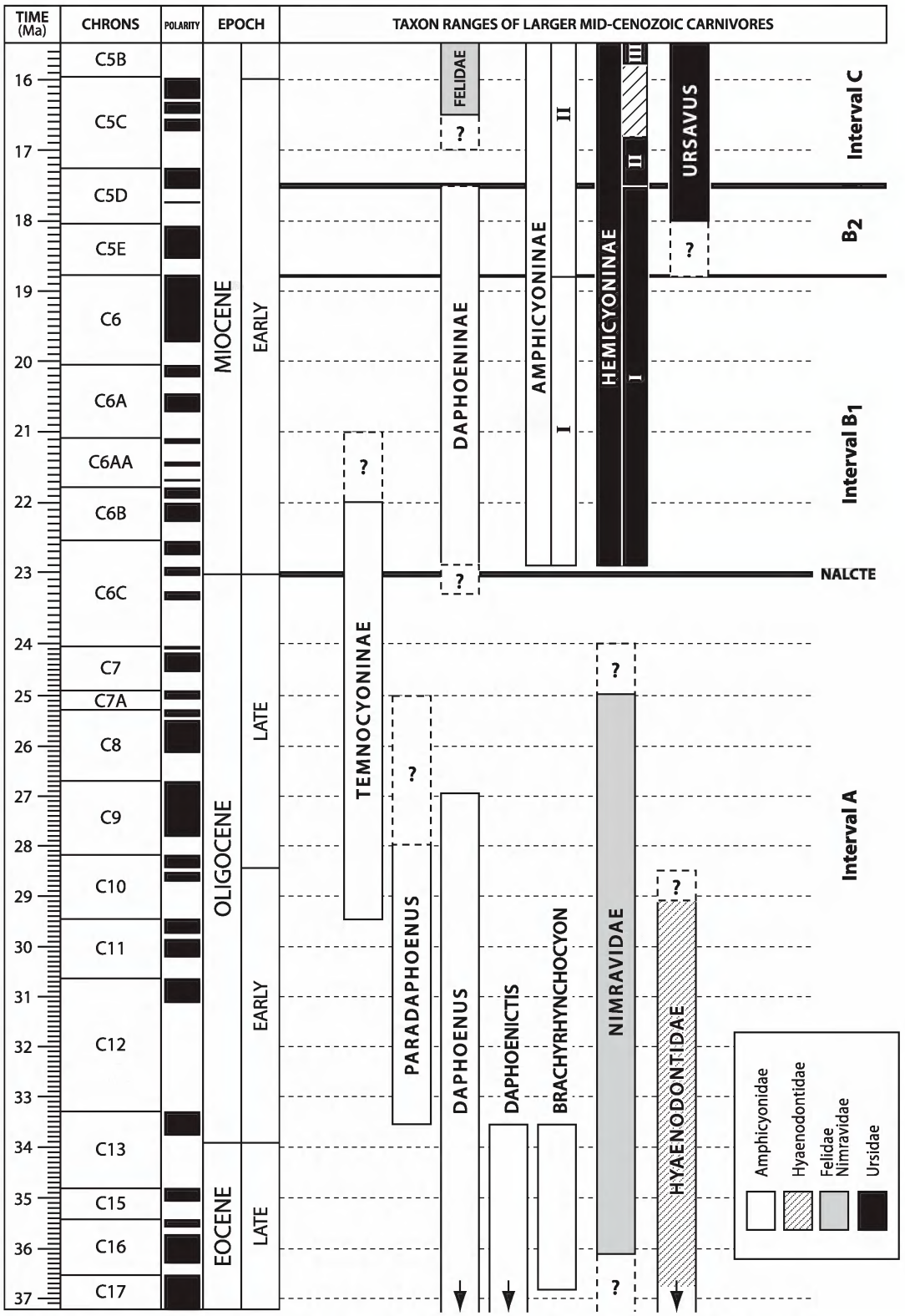
A striding or "cursorial" gait evolved several times within the large carnivores of the Oligocene and Miocene of North America. In the Oligocene, large hyaenodonts (*Hyaenodon*) developed digitigrady and cursorial tendencies despite mesaxonic fore- and hind feet and rather short fore-and hind limbs (Mellett, 1977; Gunnell, 1998). In the late Oligocene and early Miocene a different cursorial strategy was adopted by the temnocyonines, and in the early Hemingfordian a lineage of endemic daphoenine amphicyonids (*Borocyon*) evolved long-limbed predators with a fully digitigrade stance (Hunt, 2009). Also, digitigrade hemicyonine ursids migrated to the New World from Eurasia in the early Miocene and sustained their derived limb morphology until their extinction in the late Miocene (~9 Ma). However, the advanced form of digitigrady typical of canine canids developed only in the latest Miocene and Pliocene, long after the demise of earlier experiments in cursorial digitigrade carnivory by hyaenodonts, temnocyonine and daphoenine amphicyonids, and hemicyonine ursids.

This report attempts to clarify temnocyonine systematics, despite the sparse fossil record, recording dental and cranial features identifying the constitutent genera and species. Representative postcrania associated with several species indicate that the subfamily exhibited a common specialized limb and foot anatomy that apparently persisted until the termination of these lineages. The known geographic distribution of the Temnocyoninae is almost entirely limited to regions where Arikareean sediments are common and prominently exposed—the John Day Formation of north-central Oregon, and the Arikaree Group of the central Great Plains. Even in these geographic areas where rich Arikareean mammal assemblages have been found, these carnivores are extremely rare: in the 130 years since the first temnocyonines were discovered, the remains of only ~30 individuals have been conserved in museum collections (appendix 1). Temnocyonines share a similar dentition with haplocyonine amphicyonids of Europe, yet the genera in each subfamily appear to have evolved in parallel in isolation.

Abbreviations

Anatomical

AL	alisphenoid
BO	basioccipital
BS	basisphenoid


TIME (Ma)
CHRONS
POLARITY
EPOCH
TAXON RANGES OF LARGER MID-CENOZOIC CARNIVORES
C5B
C5C
C5D
C5E
C6
C6A
C6AA
C6B
C6C
C7
C7A
C8
C9
C10
C11
C12
C13
C15
C16
C17
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
MIOCENE
OLIGOCENE
EOCENE
EARLY
LATE
EARLY
LATE
FELIDAE
DAPHOENINAE
AMPHICYONINAE
HEMICYONINAE
URSAVUS
I
II
III
NALCTE
Interval C
B2
Interval B1
Interval A
TEMNOCYONINAE
PARADAPHOENUS
DAPHOENUS
DAPHOENICTIS
BRACHYRHYNCHOCYON
NIMRAVIDAE
HYAENODONTIDAE
Amphicyonidae
Hyaenodontidae
Felidae
Nimravidae
Ursidae

C (IPS)	sediment cast of inferior petrosal sinus in basioccipital
E_1, E_2	caudal entotympanics 1 and 2
EO	exoccipital
ETR	epitympanic recess
FO-AC	foramen ovale-alisphenoid canal
FR	foramen rotundum
GF	glenoid fossa of squamosal
H	hypoglossal (condyloid) foramen
M, MP	mastoid, mastoid process
M-EO	mastoid-exoccipital suture
MLF	middle lacerate foramen
P	petrosal promontorium
PC	posterior carotid foramen
PE (IPS)	posterior basioccipital embayment for inferior petrosal sinus
PGF	postglenoid foramen
PGP	postglenoid process of squamosal
PLF	posterior lacerate foramen
PP	paroccipital process
SMF	stylomastoid foramen
SQ	squamosal
T	ectotympanic

Institutional

ACM	Amherst College Museum of Natural History, Amherst, Massachusetts
AMNH	Division of Paleontology, American Museum of Natural History, New York
CM	Division of Vertebrate Fossils, Carnegie Museum of Natural History, Pittsburgh
F:AM	Frick Collection, American Museum of Natural History, New York
FMNH	Field Museum of Natural History, Chicago
LACM, CIT	Natural History Museum of Los Angeles County, Los Angeles
MNHN	Muséum national d'Histoire naturelle, Paris
NM	Northwest Museum, Portland State University, Portland, Oregon
UCMP	Museum of Paleontology, University of California, Berkeley
UF	Vertebrate Paleontology, Florida Museum of Natural History, Gainesville
UNSM	Vertebrate Paleontology, University of Nebraska State Museum, Lincoln
USNM	Department of Paleobiology, Smithsonian Institution, Washington, D.C.
TRO	Timberlane Research Organization, Lake Wales, Florida
YPM	Peabody Museum, Yale University, New Haven
YPM-PU	Princeton Collection, Peabody Museum, Yale University, New Haven
ZM	Division of Zoology, University of Nebraska State Museum, Lincoln

DISCOVERY AND GEOGRAPHIC DISTRIBUTION OF TEMNOCYONINES

John Day Basin, Oregon

Temnocyonines were first discovered in the John Day basin of Oregon. C.H. Sternberg and J.L. Wortman, collectors for E.D. Cope, recovered three specimens between 1877 and 1879. Included were two isolated rami (AMNH 6855, 6856) and a rostrum with associated mandible (AMNH 6857), all assigned to *Temnocyon altigenis*. A fourth example of this taxon was collected in 1883 by William Day for O.C. Marsh; in this case, a partial juvenile rostrum and associated ramus (USNM 7940). All had been discovered in badland outcrops of the

←

Fig. 1. Temporal range of temnocyonine amphicyonids in North America during the Paleogene-Neogene transition relative to ranges of other large carnivores (modified from Hunt, 2004, 2009, where Intervals A–C are defined: see Age and Correlation). Temnocyonine and daphoenine amphicyonids survived the North American Large Carnivore Turnover Event, placed here at the present Oligocene-Miocene boundary (Lourens et al., 2004).

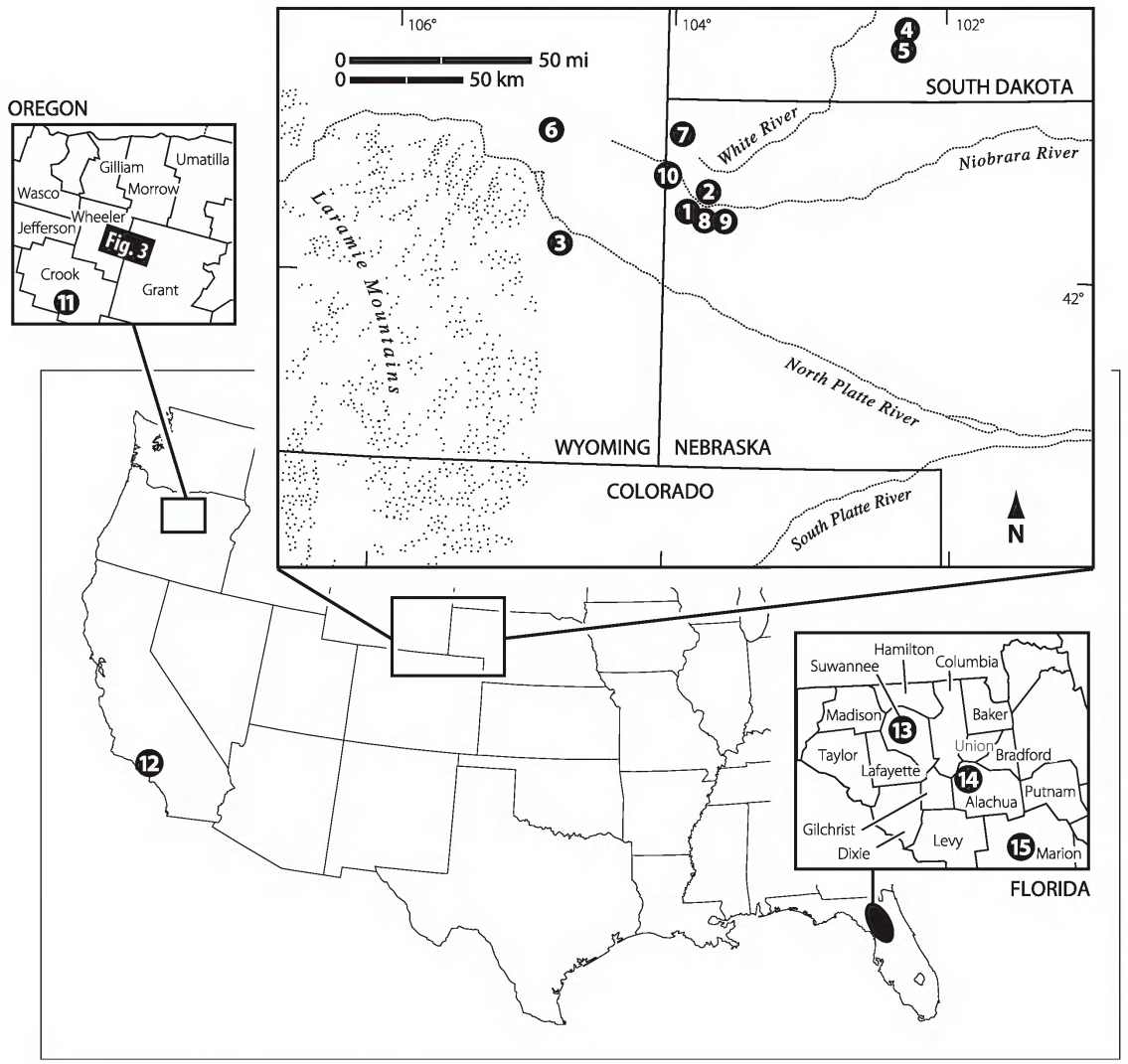


Fig. 2. Geographic distribution of temnocyonines in North America: **Great Plains—1,** *Temnocyon percussor* (*Syndyoceras* Quarry: AMNH 81005); **2,** *T. percussor* (AMNH–Cook Quarry: AMNH 81054, 81047); **3,** *Temnocyon macrogenys* (2 Mile District, near Guernsey, Wyoming: F:AM 54139); **4,** cf. *Mammacyon* (LACM loc. 1872: LACM 15908); **5,** *Mammacyon obtusidens* (Porcupine Creek, South Dakota: ACM 34-41, LACM 9194); **6,** *M. ferocior* (north of Keeline, Wyoming: F:AM 27562, F:AM 54134); **7,** *Delotrochanter petersoni* (Warbonnet Creek, Nebraska: CM 1603); **8,** *D. oryktes* (Carnegie Qu. 3, Agate Natl. Monument, Nebraska: UNSM 48700); **9,** *D. oryktes* (*Stenomylus* Qu., Agate Natl. Monument, Nebraska: ACM 4804); **10,** *D. major* (near Van Tassell, Wyoming: F:AM 27561). **Pacific Northwest—11,** Logan Butte (*Temnocyon altigenis* (UCMP 9999), see fig. 3 for other John Day localities. **California—12,** Kew Quarry. **Florida—13,** Live Oak (SB-1A); **14,** Buda; **15,** Martin-Anthony.

John Day Formation exposed along the main fork of the John Day River in the collecting district known as Turtle Cove (figs. 2, 3), with the possible exception of Cope's genoholotype ramus (AMNH 6855). These, and most later discoveries of temnocyonines, were found before the establishment of the currently accepted stratigraphic paradigm for the John Day Formation (Hay, 1963; Fisher, 1967; Fisher and Rensberger, 1972; Woodburne and Robinson, 1977; Robinson et al., 1984); consequently, a specific stratigraphic assignment for many fossils is difficult.

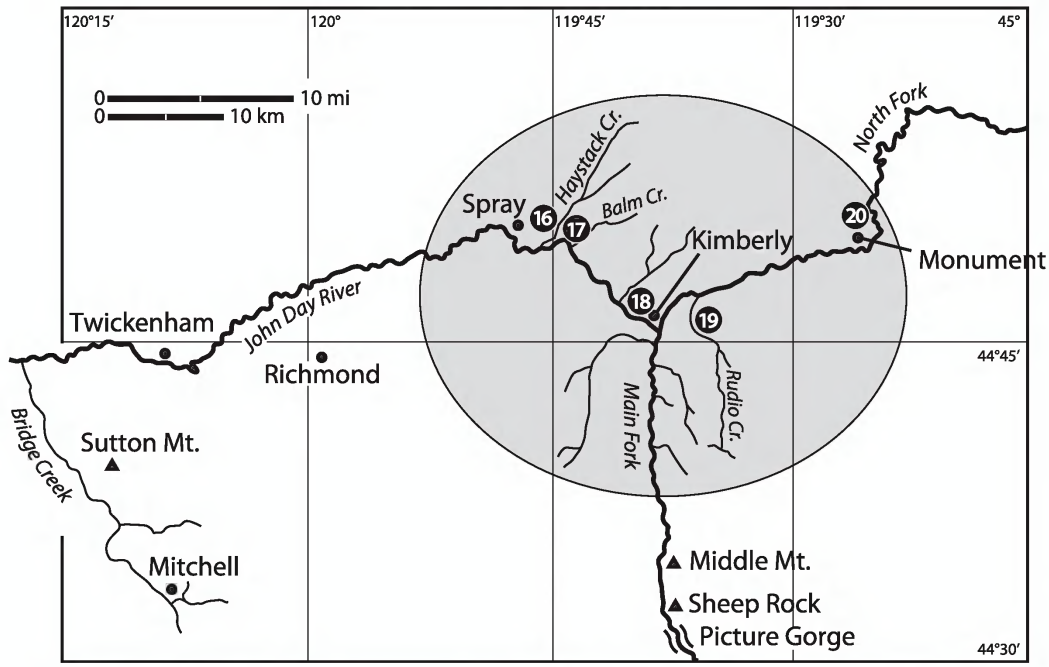


Fig. 3. Geographic distribution of temnocyonines from the John Day region of north-central Oregon. **16,** *Mammacyon obtusidens* (LACM 5386); **17,** *Temnocyon fingeruti* (NM 280/61); **18,** *Temnocyon ferox* (YPM-PU 10787); **19,** *Rudiocyon amplidens* (LACM 480); **20,** *Temnocyon altigenis* (UCMP 1549). *T. altigenis* (AMNH 6855, 6856, 6857) and *T. subferox* (YPM 10065) are from unspecified John Day Formation localities.

No complete skulls were included in these initial collections. However, the hypodigm of *Temnocyon altigenis* was soon augmented by the discovery of two crania (~17–18 cm, basilar length) during the 1899 and 1900 field expeditions of the University of California (Merriam, 1901, 1906). One was accompanied by an associated skeleton (UCMP 9999) found at Logan Butte in 1900 and was briefly discussed by Merriam (1906). Field methods employed at the time and subsequent handling resulted in some damage to the remains. Although the cranium is distorted by crushing, its particular value lies in its intact basicranium, which lacks only the auditory bullae. The other cranium (UCMP 1549) was found in 1899 southeast of the town of Monument, Oregon. It lacks the occiput and much of the basicranium but is uncrushed. One of the mandibles (AMNH 6856) in the hypodigm occludes perfectly with this cranium.

All of these John Day fossils, discovered from 1877 to 1900, were small doglike carnivorans, and comprise the most plesiomorphic species of the subfamily, *Temnocyon altigenis* Cope. The species displays what are considered primitive temnocyonine traits: (1) a carnivorous dentition with shearing carnassials, well-developed premolars, and the loss of M3; (2) deep basicranial embayments in the basioccipital for venous sinuses in which the internal carotid artery is presumed to be nested; (3) small body size (~10–15 kg); (4) absence of elongation of the lower limbs and feet (UCMP 9999), a condition that preceded limb elongation evident in several derivative temnocyonine lineages. The skull and skeleton (UCMP 9999) from Logan Butte collected by Merriam's party in 1900 is regarded as the most plesiomorphic temnocyonine, differing only slightly in its dental morphology from the amphicyonid *Daphoenus*, a plausible sister taxon. UCMP 9999 is also one of the earliest reliably dated records of the subfamily at ~29 to 29.3 Ma.

Other temnocyonines found in the John Day basin represent larger species that are plausible descendants of *T. altigenis*. Thorpe

(1922) described a skull (YPM 10065, basilar length, 21–22 cm) from the John Day Formation in the O.C. Marsh collection at Yale University. The skull was probably collected prior to 1900, conceivably between 1871 and 1877, when L.S. Davis and Wm. Day explored the John Day beds in Marsh's employ (Merriam, 1906). Cranial dimensions and dentition indicate a more advanced species than *T. altigenis*. This isolated skull (*T. subferox* n. sp., YPM 10065) retained an intact basicranium and partial auditory bulla, which Thorpe did not recognize. The bulla remnant demonstrates that only a rudimentary demibulla was present in this species, comparable to the plesiomorphic ectotympanic demibullae of the stem amphicyonids *Daphoenus* and *Cynodictis*. This would have also been the probable bulla type for *T. altigenis*, as indicated by the auditory region of UCMP 9999.

The only other large temnocyonine found in the John Day basin prior to 1900 was collected by L.S. Davis during the 1889 Princeton University expedition to the John Day beds under the direction of Wm. B. Scott. Davis discovered a nearly complete skeleton, skull (basilar length, 26 cm), and lower jaws of the largest temnocyonine found up to that time, associated with a partial oreodont skeleton in the "Upper John Day beds," Turtle Cove, later described by Eyerman (1896) as *Temnocyon ferox*. The articulated skeleton occurred in an indurated gray tuffaceous sandstone, which made preparation difficult, particularly as the crushed and fragmented bones exhibit significant diagenetic alteration. The skeleton remains today in its partially articulated state.

Since 1900 only three additional temnocyonines have been found in the John Day beds of Oregon, indicating the rarity of these carnivorans. Two were found by California Institute of Technology field parties led by Chester Stock: (a) a partial maxilla with P4–M1 (LACM 5386), from green tuffaceous claystone, John Day Formation, in Haystack Valley, Wheeler County, representing the only occurrence of *Mammacyon* in the John Day region; (b) a partial mandible of a large temnocyonine, *Rudiocyon* n. gen., associated with a crushed braincase (LACM 480), from gray tuffaceous sandstone, Kimberly Member, John Day Formation, in the valley of Rudio Creek, Grant County. *Rudiocyon* is the largest temnocyonine known from the John Day beds. These two specimens were collected shortly before 1933. No additional temnocyonines were recorded from the John Day Formation until 1986 when M. Fingerut and G. Pierson discovered an articulated skull and jaws along Balm Creek east of Haystack Valley (Hunt and Stepleton, 2004). Proximity to a radioisotopically dated bed (~23.8 Ma) demonstrated that this temnocyonine, here described as *Temnocyon fingeruti* n. sp., is the youngest occurrence of the subfamily in the Pacific Northwest.

Arikaree Group, Great Plains

Temnocyonines occur in Arikaree Group (Oligocene-early Miocene) volcaniclastic sandstones of the central Great Plains as rare isolated individuals, primarily partial mandibles with teeth. Only three relatively complete crania are known, the first found in 1934, the second in 1944, and the third in 1981. Temnocyonine fossils from the Great Plains represent a total of only 14 individuals, of which three are known from single teeth.

Three geographic areas with well-exposed Arikaree rocks have produced temnocyonines (fig. 2): (a) the Pine Ridge of Nebraska, Wyoming, and South Dakota, a prominent regional Arikaree escarpment—seven individuals extending through the stratigraphic sequence; (b) upper Arikaree rocks of Agate Fossil Beds National Monument and vicinity, Nebraska—six individuals; (c) upper Arikaree rocks of the North Platte valley near Guernsey, Wyoming—a single large temnocyonine discovered in 1939.

In May 1904, O.A. Peterson of the Carnegie Museum (Pittsburgh) discovered a pair of damaged lower jaws (CM 1603) and associated fragments of a temnocyonine, somewhat smaller than a wolf, at the Pine Ridge escarpment near the head of Warbonnet Creek, Sioux County, Nebraska. Peterson's field labels attribute CM 1603 to the "middle Monroe Creek beds," whereas his published description of the specimen (Peterson, 1907) reads "from the upper Monroe Creek horizon." Although the exact stratigraphic level is uncertain, sediment with CM

1603 shows it was collected within the upper 400 ft of the Arikaree Group in northwestern Sioux County. This was the first temnocyonine discovered in the Great Plains or, for that matter, anywhere in North America outside the John Day basin. Peterson's lack of familiarity with these carnivorans led him to simply identify it as "Family Canidae, Gen. et sp. indet." It is described here as the earliest known representative of a new genus and species, *Delotrochanter petersoni*.

In August 1904, Peterson traveled south to the 04 Ranch in central Sioux County where he, with the young rancher Harold Cook, initiated excavations that would become the incredibly rich "Agate Spring Quarries," later set aside as Agate Fossil Beds National Monument in 1965. News of the discovery led to an influx of paleontologists into Sioux County from 1905 to 1909 (Peterson, 1909). Although attention was focused on the principal bonebed exposed on University and Carnegie hills (Matthew, 1923; Peterson, 1923; Hunt, 1990), explorations along the Niobrara River near Agate eventually led to the discovery of temnocyonines in upper Arikaree rocks.

The first temnocyonine was found by Harold Cook (1909). Spurred by scientists' interest in the Agate bonebed, Cook began to search for fossils in Arikaree outcrops along the Niobrara River valley near his ranch. In 1905, he discovered mammal bones about 0.5 mile west of the Agate 04 ranch headquarters in a bluff overlooking the river. Here oreodont, horse, and rhinoceros fossils were found in the same horizon as a partial skeleton of the rare protoceratid antelope *Syndyoceras* (Barbour, 1905). These remains, attributed by Cook to the *Syndyoceras* level or "quarry," occur in the Harrison Formation ~45 ft (14 m) below its upper boundary. The site is rather nondescript, and the bones do not seem to have accumulated in a stream channel or waterhole as in the principal Agate quarries. The fossilferous level yields only scattered isolated specimens from fine-grained, gray volcaniclastic sandstone that extends for over 75 ft (23 m) along the face of the bluff. Cook continued to visit this prolific horizon and recorded his discoveries in a small notebook (titled, "Entry Catalog of Fossils, Harold J. Cook"). His entry H.C. 116 is given as "Canid gen. & sp. indet., *Syndyoceras* layer, July 1906. H.C. coll." H.C. 116 today is AMNH 81005, the partial right and left mandibles and isolated canine of a robust wolf-sized temnocyonine, later described by Cook (1909) as the holotype of *Temnocyon percussor*. Although there remains some question about the attribution of AMNH 81005 to the *Syndyoceras* level, the weight of evidence indicates it came from that site.

Two years later, in July 1908, Harold Cook found an isolated M1 in the American Museum–Cook Quarry (H.C. 1197, AMNH 81047), which he identified as "carnivore." This is the only known upper molar of *Temnocyon percussor*, a determination based on the occlusal form of lower molars of AMNH 81005. In August 1909, a lower carnassial (H.C. 229, AMNH 81054) of *T. percussor* was collected by Cook from the same quarry. These fossils (AMNH 81005, 81047, 81054) indicate a species similar to yet somewhat larger than *T. ferox* of the John Day beds. The American Museum–Cook Quarry occurs in the basal Anderson Ranch Formation (Hunt, 2002b), 2 mi north of the Agate waterhole bonebed on Carnegie Hill, and at the same stratigraphic level. The quarry is 45–50 ft (14–15 m) stratigraphically above the *Syndyoceras* level (Hunt, 1990: fig. 4). The *Syndyoceras* locality and the American Museum–Cook Quarry today remain outside the boundaries of the Agate Fossil Beds National Monument on private land and are the only localities where *T. percussor* has been found.

In 1939 Charles Falkenbach of the Frick Laboratory excavated a mandible and postcranial fragments of a huge temnocyonine (F:AM 54139) from Arikaree rocks near Guernsey, Platte County, Wyoming. Although Falkenbach did not record the exact location, Frick Laboratory records show that this individual probably came from upper Arikaree beds a few miles south of the North Platte River referrable to the Anderson Ranch Formation. The teeth indicate affinity with *T. percussor* from Agate. This taxon, *Temnocyon macrogenys* n. sp., represents the terminal species of a dentally plesiomorphic lineage of carnivorous temnocyonines in which the cusp pattern of the teeth can be derived from the teeth of *T. altigenis*.

In addition to the small sample of *Temnocyon percussor* from the vicinity of Agate Fossil Beds National Monument, more complete material of four individuals belonging to a different temnocyonine lineage, *Delotrochanter* n. gen., was found within the present boundaries of the monument, first by Amherst College in 1909 at *Stenomylus* Quarry, then by Princeton University in 1914 in the Carnegie Hill bonebed, and finally in 1981 by the University of Nebraska working in the carnivore dens at Beardog Hill.

In 1909, while collecting at *Stenomylus* Quarry, F.B. Loomis (Amherst College) and his party found a large amphicyonid skeleton (ACM 4804) that he believed to be *Daphoenodon superbus*, the large beardog found in the carnivore dens at Beardog Hill (Loomis, 1910; Peterson, 1910; Hunt et al., 1983). However, Loomis was mistaken: the skeleton represents a previously unrecognized cursorial temnocyonine, *Delotrochanter oryktes* n. gen., n. sp. The skeleton was never described by Loomis and was damaged when it was pressed into a wall of wet plaster at the Amherst College Museum shortly after it was collected. It was later carefully removed by Dr. Margery Coombs for study by a graduate student, Mildred Schlain (Schlain, 1980), and is one of the most complete temnocyonine skeletons yet discovered. Some bones of a juvenile (ACM 4804A) were associated with the skeleton of the adult.

In 1914 Princeton University removed a section of the waterhole bonebed on Carnegie Hill for exhibition in their museum. This slab eventually was transferred to Yale University where it was cataloged as YPM 12213. Although carnivores are uncommon in the bonebed, a calcaneum referrable to *D. oryktes* (YPM 24872) was found in this slab, the only record of a temnocyonine from the waterhole itself.

In September 1981, UNSM investigators at Agate Fossil Beds National Monument relocated O.A. Peterson's Quarry 3 on Beardog Hill, which in 1904–1905 yielded abundant carnivore material (amphicyonids, canids, and mustelids). One of the first items recovered was a fragment of a temnocyonine upper molar, which ultimately led to the crushed skull and postcranial remains of a large temnocyonine (UNSM 47800) lying within a burrow, one of several making up a den complex (front cover and fig. 37B; also Hunt et al., 1983: fig. 1, burrow C). This individual proved similar to the temnocyonine from *Stenomylus* Quarry found by Loomis in 1909, and both are referred here to *D. oryktes*. The presence of *Delotrochanter oryktes* in these dens together with multiple skeletons of *Daphoenodon superbus* demonstrated their coexistence in the region during the early Miocene.

Upper Arikaree rocks exposed in the Niobrara River valley at Agate Fossil Beds National Monument can be traced northwest through Sioux County into Niobrara County in southeastern Wyoming. Here, near the town of Van Tassell, Paul Miller in 1927 found fragmented lower jaws and a few upper teeth of a large temnocyonine (F:AM 27561), *Delotrochanter major* n. sp., a dentally more advanced descendant of *D. oryktes*. Its stratigraphic occurrence was not well documented by Miller, but pale reddish-brown, fine-grained sediment associated with the remains indicates its derivation from Peterson's "Upper Harrison" beds near Van Tassell (now Anderson Ranch Formation, Hunt, 2002b), possibly from the stratotype section itself. Thus, the biochron of *Delotrochanter* in the Great Plains involves three species: (a) *D. petersoni* n. sp., the jaws (CM 1603) found by O.A. Peterson in 1904 near the head of Warbonnet Creek in Sioux County, and the earliest representative of the genus in the Great Plains; (b) *D. oryktes* n. sp., occurring at Agate Fossil Beds National Monument—the genotypic species including the most complete material; and (c) Van Tassell *Delotrochanter major* n. sp., the terminal occurrence of the lineage in North America.

Arikaree rocks of the Pine Ridge escarpment have produced remains of a third temnocyonine lineage, *Mammacyon*, which became extinct before the early Miocene when *Delotrochanter* and *Temnocyon* still survived in the Great Plains. In 1934 F.B. Loomis collected from the Wounded Knee area of South Dakota a crushed skull and partial skeleton (ACM 34–41) of a temnocyonine somewhat larger than a wolf but with heavy blunt-cusped cheek teeth, suggestive of a durophagous habit. This dental

morphology caused Loomis to name the taxon *Mammacyon obtusidens* in reference to the pestlelike cusps. No jaw was found with the skull, but in 1964 Harley Garbani collected a mandible (LACM 9194) in the Monroe Creek Formation of the Wounded Knee area that can be assigned to the same species. The skull of ACM 34–41 included the basicranium and was only the second temnocyonine to retain the auditory bulla.

A similar but much larger skull and partial mandible of *Mammocyon* were found by Charles Falkenbach of the Frick Laboratory in younger Arikaree rocks of the Pine Ridge escarpment north of Keeline, in Niobrara County, Wyoming. The mandible and skull were not associated but occlude satisfactorily, share a complementary cusp morphology, and are assigned here to the same species, *M. ferocior* n. sp. The mandible (F:AM 27562) was found in 1931, and the magnificent skull (F:AM 54134) 13 years later in 1944; a partial postcranial skeleton is associated with the mandible and indicates cursorial tendencies. This large species marks the termination of the *Mammocyon* lineage in the Great Plains.

The Oligocene Sharps Formation in the Wounded Knee area, South Dakota, has produced a mandibular fragment with two molars (LACM 15908) that probably represents the earliest occurrence of *Mammocyon*. Found in 1963 by J. Harksen, this specimen represents both the smallest individual and the lowest stratigraphic record of a temnocyonine in the Great Plains. It was first mentioned by Macdonald (1970: 60) who referred it to the canid genus *Sunkahetanka*. Despite its early appearance, its teeth are larger and m1–2 more derived than specimens of *Temnocyon altigenis* from the John Day basin, suggesting that the John Day sample from the Turtle Cove area is chronologically older than the level in the Sharps Formation that produced LACM 15908.

Kew Quarry, California

The only temnocyonine from western North America found outside the John Day region is represented by a badly crushed and fragmented lower jaw (LACM 470), collected in Kew Quarry, Las Posas Hills, California by Thurston in 1930 (fig. 2). Associated mammals have indicated either a late Whitneyan or early Arikareean age for the Kew Quarry assemblage (Prothero et al., 1996). The temnocyonine mandible and dentition are difficult to reconcile with a late Whitneyan age: the cheek teeth are somewhat larger and more derived than in any individual from the early Arikareean John Day *T. altigenis* sample, including Cope's holotype. The teeth of LACM 470 occlude appropriately with the upper dentition of *Temnocyon subferox* and could represent that species. Here the Kew Quarry temnocyonine is assigned to *Temnocyon* cf. *T. subferox*. Prothero et al. (1996: 183) suggested that an age in the interval 28.7–29.3 Ma seemed reasonable, which relies heavily on the carnivores from the quarry and correlation to Global Polarity Chron 10r (see Age and Correlation).

Live Oak and Martin-Anthony Sites, Florida

Arikareean localities in Florida have produced a few rare temnocyonine fossils discovered in 1966 and 1974–75 (fig. 2). Other reports of *Temnocyon* in Florida in the scientific literature (e.g., Olsen, 1958: 595—fossils now referred to *Daphoenodon notionastes*) are inaccurate and have been found to be canids or other genera of amphicyonids. The few teeth that are known are adequate to demonstrate the existence of Temnocyoninae in southeastern North America in the Arikareean, but these fossils can only be tentatively assigned to genera recognized in the Great Plains and John Day basin of Oregon.

Frailey (1978) described a temnocyonine M1 (TRO 390) from the Live Oak locality (SB-1A), north-central Florida. The site is a limestone mine: in the mining pits, sediments overlying the Suwanee Limestone have yielded fossil mammals from the fine interstitial matrix of an unstratified, poorly sorted limestone conglomerate (Frailey, 1978). The form of this M1 is more derived than any M1 attributed to *Temnocyon* and is most similar to the M1 of *Delotrochanter oryktes* from *Stenomylus* Quarry. If so, the tooth would come from a slightly smaller, less advanced species. Referral to *Mammacyon* is less likely but cannot be ruled out. Also found at Live

Oak is a temnocyonine unciform (TRO 661), lower canine (TRO 388), and two phalanges (TRO 386, 387) that correspond in size to the M1 and likely represent the same species. The temnocyonine unciform is most similar to the unciform of the wolf (*Canis lupus*) among living carnivores in contrast to the taller, narrow unciforms of living ursids and felids. The unciform compares closely with that bone in *Temnocyon ferox*, and also *D. oryktes* described by Schlain (1980), and shows that the Live Oak carnivore was much larger than *T. ferox* and only slightly smaller than *D. oryktes*. This temnocyonine and *D. notionastes* occur together at Live Oak.

MacFadden (1980) mentioned a temnocyonine M2 (UF 24203) found at the Martin-Anthony locality in northern Florida in 1966. Clastic sediments assigned to the Hawthorne Group at this site have yielded not only the M2 but also turtles, dugongs, a rhinoceros, and a small camelid. These sediments have been allocated to the Penney Farms Formation, the basal unit of the Hawthorn Group at this locality (Scott, 1988). A strontium isotope age of ~24.6 Ma derived from molluscs in the underlying limestone bed at Martin-Anthony could approximate the age of the temnocyonine molar. A late Oligocene age is not improbable because the M2, a large tooth, compares most closely with M2s of *Mammacyon ferocior* and *M. obtusidens*. However, M2 is not yet known for the larger species of *Temnocyon* (*T. percussor*, *T. macrogenys*) and *Delotrochanter* (*D. major*).

Frailey (1979: 143) described a calcaneum (UF 16908) from the Buda local fauna, Alachua County, north Florida, as an Arikareean felid; at that time the similarity between the calcanea of felids and temnocyonines was not recognized. This calcaneum is the only record of a temnocyonine in the Buda fauna where this species also occurs with *D. notionastes*. It shows the tall, narrow axial form, elongate distal region, and high sustentaculum typical of the subfamily, details already evident in the calcaneum of the plesiomorphic *T. altigenis* from Logan Butte. Although a generic or specific assignment is not possible because of the near anatomical identity of temnocyonine calcanea, its form indicates a carnivore of the size of *Temnocyon ferox*. UF 16908 is 22% larger than the calcaneum of *T. altigenis* (UCMP 9999), 11% smaller than that of *D. oryktes* (UNSM 48700), and 22% smaller than that of *Mammacyon ferocior* (F:AM 27562).

More complete material of Florida temnocyonines is required to place them confidently within lineages recognized elsewhere in North America. However, the M1 and calcaneum suggest an age prior to the latest Arikareean (Ar 4) for the Live Oak and Buda sites.

IDENTIFICATION OF TEMNOCYONINE LINEAGES

North American temnocyonines range from the latest early Oligocene to early Miocene, species in each lineage attaining their largest size as they approach extinction. Dentitions provide the strongest evidence for the existence of discrete temnocyonine lineages (fig. 70). Three genera are recognized in the John Day Formation of Oregon (*Temnocyon*, *Rudicyon* n. gen., *Mammacyon*), and three in the Arikaree Group of the Great Plains (*Temnocyon*, *Mammacyon, Delotrochanter* n. gen.). Only *Temnocyon* and *Delotrochanter* extend into the early Miocene in the Great Plains. Temnocyonines are unknown in the Miocene except for the Great Plains occurrences. Previously, lineages within the subfamily have been difficult to identify, due to scarcity of material, and the distribution of fossils among a number of different collections. Although the known sample of temnocyonines still remains small, recent radioisotopic dating and stratigraphic studies in the Great Plains and in the John Day basin have provided the necessary foundation for evaluating and comparing specimens.

This study is based on simultaneous examination of all North American temnocyonine fossils: comparison was greatly facilitated by viewing the entire sample in one location. This resulted in recognition of three dentally specialized and geochronologically young end-member species (*Temnocyon macrogenys* n. sp., *Delotrochanter major* n. gen. et sp., *Mammacyon ferocior* n. sp.), which then were traced backward in time into older rocks. The terminal species of *Temnocyon* and *Delotrachanter* occur in the latest Arikareean (Ar4); the terminal species of *Mammacyon*, *M. ferocior*, is found in the upper Arikaree

Group of Wyoming and is believed to be earliest late Arikareean in age (Ar3).

Future students of the group may find that these lineages require modification in the light of new fossil discoveries. Because of the small number of fossils, intraspecific variation in temnocyonines cannot be adequately addressed by this study, particularly dental variation. If species eventually prove highly variable in dental features, then the fossils discussed here may have been split into an excessive number of morphospecies. However, based upon dental variation among living carnivorans, and that observed in the stem temnocyonine, *Temnocyon altigenis*, the variation permitted in species described in this report is not exceptional.

Table 1 presents the diagnostic differences used to recognize these genera. These involve the teeth: (1) size and form of the premolars; (2) proportions of the upper and lower carnassials; (3) cusp pattern of the lower carnassial, including presence or absence of the metaconid; (4) form of the first upper molar; (5) length and configuration of m2. These features, singly or in combination, define the genera. The genera *Mammacyon* and *Delotrochanter* are phyletic lineages or clades; *Temnocyon* is a paraphyletic genus that includes the ancestry of the subfamily and its descendants retaining plesiomorphic craniodental features—species in the genus differ in size and autapomorphic dental traits. Within each genus there is an evident increase in body size over time best reflected in skull size and dimensions of the mandibular (table 2) and maxillary (table 3) dentitions.

PREMOLARS: Tall, laterally compressed premolars first observed in John Day temnocyonines by E.D. Cope are one of the most evident diagnostic traits of the subfamily. Cope's genoholotype mandible of *Temnocyon,* as well as those of all other plesiomorphic temnocyonines, features tall well-developed p2–4 and P2–3. P1/p1 are small, often low and peglike teeth that lack the height of the more posterior premolars and are not replaced by a second-generation tooth (they belong to the milk dentition as in many other mammals). In *Temnocyon* and *Mammacyon* the upper and lower premolars (except of course P4) are typically triangular (in lateral view), narrow, elongate teeth, and are not shortened or widened. This is also true for the only surviving premolar of *Rudiocyon*. *Delotrochanter* on the other hand has short, posteriorly wide premolars, distinguishing it from *Mammacyon* and *Temnocyon*. *Temnocyon* and *Mammacyon* also lack a well-defined posterior accessory cusp on the posterior slope of p3, whereas *Delotrochanter* has such a cusp. Premolars increase in size as body size increases within all lineages; however in *Delotrochanter* there is a trend toward short, wide premolars, whereas in *Temnocyon* and *Mammacyon* the longer, relatively narrow teeth are maintained (except for a broad p4 in *Mammacyon ferocior*). Premolars (p1–4) increase in size posteriorly in the toothrow, and p4 is often of striking size relative to m1. These robust premolars accompany crushing carnassials and molars, particularly in the large terminal species of *Mammacyon* and *Delotrochanter*, suggesting a durophagous adaptation. The prominent premolars of temnocyonines distinguish them from amphicyonines, which have greatly reduced p2–3/P2–3.

CARNASSIALS: One of the most diagnostic temnocyonine teeth is the upper carnassial. Initially in early John Day temnocyonines this tooth is little different in form from the shearing upper carnassial of a typical plesiomorphic beardog like *Daphoenus*. However, in *Delotrochanter* and *Mammacyon* the upper carnassial evolves into an enlarged, blunt-cusped crushing tooth in which shear is no longer the principal function. This is accomplished by shortening of the metastylar blade (thus metastylar shear is diminished), while the protocone region becomes lingually extended and much enlarged, and the protocone itself transforms into a blunt pestlelike cusp (table 4). The occlusal outline of the upper carnassial thus takes the form of an equilateral triangle, not the more common isosceles triangle found in most arctoid and cynoid carnivorans with a shearing P4. Whether this same trend occurred in *Temnocyon* remains to be demonstrated because the large end-member species of that genus from the Great Plains (*T. macrogenys*) is not known from specimens that preserve the upper carnassial. The terminal species of John Day *Temnocyon* (*T. fingeruti*, *T. ferox*) suggest that such modification occurred but

TABLE 1
Comparison of Dental Traits of North American Temnocyoninae

	Temnocyon	*Delotrochanter*	*Mammacyon*
c, C	Upper and lower canines show no evident differences among the 3 genera. Upper canines are less recurved than lower canines. Strong enamel ridges run along the posterior face and the anterointernal face in these genera. These two ridges are also present on the lower canine, however, the more posterior ridge is placed on the posterointernal border and the canine itself is rotated clockwise in dorsal view.		
p1	No evident differences in this tooth allow discrimination among the genera. It is small, low, single-cusped, and single-rooted, with a longer posterior slope. The milk dentition in a juvenile of *T. altigenis* demonstrates that p1/P1 erupt as part of the deciduous dentition and are not replaced in the adult.		
p2	In the John Day holotype of *T. altigenis* Cope and other specimens of the species hypodigm, this tooth is tall, laterally compressed, without a posterior accessory cusp (PAC). The *Temnocyon* p2 retains this simple form yet becomes taller in *T. ferox* and *T. macrogenys*. The p2 of *Temnocyon* is difficult to distinguish from p2 of *Mammacyon* without the remainder of the dentition. In *Delotrochanter* the p2 is short, posteriorly wide, without PAC, and with a steep anterior face; the anterior root is much smaller than the posterior root, which differs in this regard from the equi-sized roots of the other genera.		
p3	Simple triangular tooth without PAC, not significantly widened posteriorly	Robust anteroposteriorly short triangular tooth, with PAC, posteriorly widened	Simple triangular tooth without PAC, elongate, widened posteriorly only in *M. ferocior*, the terminal species
p4	Tall, triangular, laterally compressed tooth, robust, with strong PAC placed toward *labial* side about halfway up posterior face; shelflike posterior cingulum with small cusp	Shorter posteriorly wide tooth with enlarged PAC that is *centrally* located on posterior face; posterior cingulum shelf absent or very abbreviated, and cusp on remnant of shelf applied closely against PAC	Similar to *Temnocyon* tooth but not as tall; PAC placed toward *labial* side on posterior face; shelflike posterior cingulum with small cusp
m1	*With* metaconid; basal labial cingulum *sinuous*; para- proto-hypoconid not aligned; no notch at posterointernal corner of talonid (talonid border convex)	*Without* metaconid; basal labial cingulum nearly *straight*; para-proto- hypoconid aligned; hypoconid enlarged; weak notch at posterointernal corner of talonid	*Without* metaconid (vestigial in LACM 15908); basal labial cingulum *sinuous*; para- proto- hypoconid not aligned; strong internal notch at posterointernal corner of talonid
m2	Short relative to m1 with protoconid taller and larger than hypoconid	Short relative to m1 with protoconid and hypoconid about equal in size and height	Elongate relative to m1 with protoconid and hypoconid about equal in size and height
m3	Known in only three individuals in which no significant differences can be identified.		
P1	No evident differences in this tooth allow discrimination among the genera. It is small, low, single-cusped, and single-rooted. In *T. ferox* (YPM-PU 10787), P1 is a triangular, more bladelike tooth; in *M. ferocior* (F:AM 54134) it is a simple large peg.		
P2	Laterally compressed triangular tooth with slightly elongated posterior part; no PAC	Triangular tooth, shorter and posteriorly wider than in *Temnocyon* and *Mammacyon*; no PAC	Laterally compressed triangular tooth with somewhat widened posterior part; no PAC (P2 known only in *M. obtusidens*)
P3	Laterally compressed triangular tooth with somewhat widened posterior part; small PAC present	Triangular tooth, shorter and posteriorly wider than in *Temnocyon* and *Mammacyon*; small PAC on labial side of expanded posterior part of tooth	Laterally compressed triangular tooth with somewhat widened posterior part; PAC absent or very small (P3 known only in *M. obtusidens*)
P4	*T. altigenis* retains plesiomorphic form of amphicyonid P4 in which protocone is anteriorly placed and metastylar blade is not abbreviated; *T. ferox* damaged but like *T. altigenis*; P4 unknown in *T. macrogenys* but probably as in *T. altigenis*	Protocone region enlarged but not extended lingually beyond internal border of M1; metastylar blade short; tooth robust and blunt-cusped, and smaller than *Mammacyon* P4; parastylar region less anteriorly extended than in *Mammacyon*	Protocone region greatly enlarged and extended lingually beyond internal border of M1; metastylar blade short; tooth robust and blunt-cusped, and relatively larger than *Delotrochanter* P4; parastylar region strongly anteriorly extended

TABLE 1
(Continued)

	Temnocyon	*Delotrochanter*	*Mammacyon*
M1	*T. altigenis* retains plesiomorphic M1 form (UCMP 9999) with little or no anteroposterior widening of protocone region; although some protocone expansion occurs in later *Temnocyon* species (*T. percussor*, *T. ferox*), it is much less than in *Mammacyon* and *Delotrochanter*	M1 with pronounced thickening of lingual cingulum resulting in anteroposterior widening of protocone region relative to the length of the labial margin of M1	M1 with pronounced thickening of lingual cingulum resulting in anteroposterior widening of protocone region relative to the length of the labial margin of M1; labial M1 margin also extended
M2	In all genera M2 is significantly smaller than M1 and occlusal form is variable; metacone greatly reduced relative to paracone as body size increases; lingual border of M2 at about same level as that of M1 in *Temnocyon* whereas in *Mammacyon* and *Delotrochanter* the M2 lingual margin appears labially retracted due to transverse expansion of the M1 lingual cingulum; M2 occlusal form more rectangular with parallel straight anterior and posterior margins in *Delotrochanter oryktes* and *Mammacyon*; M2 with labial and lingual halves "folded" nearly at right angle in *Mammacyon obtusidens* yet less so in *M. ferocior and Delotrochanter oryktes.*		
M3	Absent	Absent	Absent

was not as pronounced as in the other two genera.

The lower carnassial alters its cusp pattern and proportions in both *Delotrochanter* and *Mammacyon* (and in *Rudiocyon*) but only minor changes occur in *Temnocyon*. Early John Day temnocyonines (*T. altigenis*) have lower carnassials that closely approach a plesiomorphic shearing amphicyonid m1 (e.g., *Daphoenus vetus*). This plesiomorphic pattern in *Daphoenus* incorporates a prominent tricuspid trigonid with well-developed paraconid-protoconid shear and a distinct metaconid; the talonid lies at a lower level than the trigonid and forms a shallow basin bordered labially by a prominent hypoconid and lingually by a thin enamel rim often with a tiny entoconid cusp. In early John Day temnocyonines the only significant modification of this plesiomorphic pattern is the loss of the entoconid and development of an enlarged hypoconid that occupies nearly the entire talonid. Consequently in the earliest temnocyonines the m1 talonid is already a blunt crushing instrument.

As the three lineages evolve, only two (*Delotrochanter*, *Mammacyon*) show significant changes in m1 cusp pattern and form. *Temnocyon* does not and m1 simply becomes larger: even its terminal latest Arikareean species (*T. macrogenys*) still retains the plesiomorphic m1 cusp pattern (tall trigonid with metaconid, and low talonid with enlarged blunt hypoconid). The most pronounced modification of m1 occurs in *Delotrochanter* in which the metaconid is lost even in the oldest species (*D. petersoni*); the paraconid and hypoconid approach each other in height; and the hypoconid becomes an enlarged bulbous cusp occupying the entire talonid. The talonid becomes enlarged to such a degree that in the terminal species, *D. major*, the hypoconid exceeds the paraconid in size.

The terminal species of *Temnocyon* and *Delotrochanter* (*T. macrogenys*, *D. major*), which coexisted in the latest Arikareean (Ar4) of the central Great Plains, demonstrate the divergent extremes attained by the lower carnassial. The former retains an enlarged, massive plesiomorphic m1; the latter a completely transformed crushing tooth. However, the lower carnassials of *Mammacyon* and *Delotrochanter* are less readily distinguished since in both genera the metaconid is lost early, and the paraconid and hypoconid tend to approach each other in height. Isolated lower carnassials of the two genera may be identified by the larger, more expanded talonid and hypoconid in *Delotrochanter* and the form of the labial cingulum, which is straight in *Delotrochanter* and sinuous in *Mammacyon*. In addition to loss of the metaconid, the m1 paraconid-protoconid cusps in *Mammacyon* and *Delotrochanter* become more rounded and less sectorial. *Delotrochanter major* represents the

TABLE 2
Measurements (length × width, mm) of the Mandibular Dentition of Temnocyoninae

Taxon	p2	p3	p4	m1	m2	c–m2	p1–4
Temnocyon altigenis							
AMNH 6855*	10.7 × 4.6	12.5 × 5.4	15.1 × 6.8	19.0 × 9.3	11.3 × 6.6	78.7	47.0
AMNH 6856	10.2 × 4.9	11.8e × —	14.3 × 6.7	18.5 × 8.9	10.1 × 6.3	76.1e	44e
AMNH 6857	10.4e × 4.7e	13.0 × 5.7	15.0 × 6.5	19.5 × —			46.6
USNM 7940				18.4e × 8.6	10.6 × 6.5e		
UCMP 9999	10.0 × 4.5	11.9 × 4.8	14.1 × 6.1	17.4 × 7.7	10.4 × 6.2	71.8	43.9
Temnocyon cf. *T. subferox*							
LACM 470	12.6e × —	14.7 × 7.4	15.6 × 7.6e	20.2e × 10.4	11.5e × 7.2	80e	48.6
Temnocyon fingeruti, new species							
NM 280/61*	12.1 × 5.6	15.3 × 6.6	19.3 × 8.7	24.7 × 10.6	14.8 × 8.9	108.7	65.4
Temnocyon ferox							
YPM-PU 10787*	14.6 × 6.2	16.6e × 7.4e	18.6 × 8.3	22.2 × 10.7	12.4 × 7.9	101.9	59.1
Temnocyon percussor							
AMNH 81005*	14.8a × 7.2a	15.9 × 7.8	19.7 × 9.0	23.5 × 10.5	13.9 × 9.0	110.9	63.3
AMNH 81054				24.2 × 10.8			
Temnocyon macrogenys, new species							
F:AM 54139*	16.6 × 8.5	abnormal	22.1 × 10.4	28.2 × 13.0	17.4 × 10.4	125.9	81.6
Rudiocyon amplidens, new species							
LACM 480*			22.4 × 9.9	28.7 × 13.2	15.2 × 9.1		
Mammacyon obtusidens							
LACM 9194	14.4 × 6.4	17.7 × 7.8	20.4 × 9.7	24.4 × 11.4	15.5 × 9.6	98.3	58.2
Mammacyon ferocior, new species							
F:AM 27562*	17.9 × 8.1	19.3 × 9.0	21.9 × 10.7	27.7 × 13.0e	17.3 × 10.3	120.0	74.3
cf. *Mammacyon*							
LACM 15908				20.5 × 9.9	12.0 × 7.5		
Delotrochanter petersoni, new species							
CM 1603*	12.2a × 6.6a	13.7a × 6.6a	16.7a × 7.2a	22.3 × 11.3		92e	49e
Delotrochanter oryktes, new species							
ACM 4804*	14.9 × 8.2	16.6 × 9.4	21.0 × 10.8	27.1 × 12.7	16.0 × 10.0	98.8	59.7
Delotrochanter major, new species							
F:AM 27561*	>14 × >7.2	17.7 × 10.2	21.6 × 12.3	28.0 × 14.1	17.1e × 10.6	115e	72e

*= holotype, e = estimated measurement, a = alveolar measurement.

extreme expression of this trend: the lower carnassial is little more than three linearly arranged, rounded cusps (with paraconid slightly offset lingually from the protoconid; paraconid-hypoconid nearly equal in height), creating a formidable crushing instrument when coupled with the robust premolars. In *Mammacyon ferocior* the m1 is modified in similar fashion but fails to attain the size and degree of simplification seen in *D. major*.

FIRST UPPER MOLAR: This tooth, together with P4, is particularly diagnostic for Temnocyoninae. Even the most plesiomorphic species from the John Day basin can be identified as members of the subfamily by the form of the M1 protocone isolated on an enamel flat surrounded by a thickened lingual cingulum. In the larger, dentally derived species of *Mammacyon* and *Delotrochanter* the protocone evolves to a prominent isolated knoblike cusp; the enamel flat is conspicuously enlarged; and the lingual cingulum is thicker and more prominent. A ratio of the anteroposterior length of the

TABLE 3
Measurements (length × width, mm) of the Maxillary Dentition of Temnocyoninae

Taxon	P2	P3	P4	M1	M2
Temnocyon altigenis					
UCMP 9999	10.5 × 4.6	12.2 × 5.8	16.5 × 12.1	13.8 × 19.5	7.1 × 12.0
AMNH 6857			19.1 × 12.6e	14.0 × 21.5e	8.0 × 13.8
USNM 7940			16.9 × 12.7	13.8 × 20.5	8.7e × 13.0e
UCMP 1549	10.9e × 4.6	12.8e × 5.9	17.8e × 13.2e	13.5e × 18.7e	8.4e × 12.0
Temnocyon subferox, new species					
YPM 10065*		12.9 × 6.6	19.3 × 14.4	14.7 × 20.6	8.3 × 13.0
Temnocyon fingeruti, new species					
NM 280/61*	13.4 × 5.7	16.1 × 7.0	22.0 × 15.4	17.1 × 22.4	9.6 × 17.4
Temnocyon ferox					
YPM-PU 10787*	13.9 × 6.3	16.6 × 7.8	22.2e × 16.5	18.2 × 23.9	8.4 × 13.6
Temnocyon percussor					
AMNH 81047				20.9 × 27.9	
Mammacyon obtusidens					
ACM 34-41*	18.5 × 7.7	20.3 × 10.6	25.2 × 21.5	20.4 × 28.2	10.5 × 17.9
LACM 5386			21.8 × 18.2	17.8 × 24.8e	
Mammacyon ferocior, new species					
F:AM 54134	18.6a × 9.4a	21.1a × 13.4a	26.0 × 23.1	21.4 × 29.8	10.8 × 17.4
Delotrochanter oryktes, new species					
ACM 4804*	15.8 × 8.7	18e × —	21.4 × 18.8	17.7 × 25.4	9.3 × 17.4
UNSM 47800	15.9 × 8.0	18.2 × 9.8	22.8 × 17.9	17.5 × 23.9	8.9 × 15.3
cf. *Delotrochanter*					
TRO 390				17.6 × 23.5	
Delotrochanter major, new species					
F:AM 27561*	17.0 × 9.0	18.7 × 11.9	23.5 × 19.8		

*= holotype, e = estimated measurement, a = alveolar measurement.

labial margin compared to the length of the lingual half of the tooth measures this change in M1 form in temnocyonines (table 5).

The M1 of *Temnocyon* is unknown in the terminal species, *T. macrogenys*; it probably did not differ from the plesiomorphic form still retained in *T. percussor*, one of the youngest species of *Temnocyon* in which M1 is preserved and the probable predecessor to *T. macrogenys*. The plesiomorphic M1 of *T. altigenis* (Logan Butte) is only slightly modified in *T. percussor* and *T. ferox*, less so in *T. fingeruti*. These species lack the blunt knob-like cusp seen in *Mammacyon* and *Delotrochanter*, maintaining a preprotocrista diverging from the more normally configured protocone (a postprotocrista may also occur).

SECOND LOWER MOLAR: Species of *Temnocyon* preserve the plesiomorphic cusp pattern of this tooth in which the protoconid and hypoconid are situated at the labial margin. In contrast, the m2 of *Mammacyon* and *Delotrochanter* share a derived condition in which a rather blunt protoconid and hypoconid, placed one behind the other, are situated in the center of the tooth so that the former cusp fills the trigonid and the latter occupies the talonid.

In other respects this tooth is one of the more variable elements of the temnocyonine dentition. It is unwise to attribute too much significance to slight differences in m2 form. However, *Mammacyon* includes large carnivorans with a definitely elongate, rectangular m2 (table 6, ratio E/F), and this trait, coupled with the m1 form and the elongate, narrow premolars, identifies the lineage dentally. Furthermore, a small notch or indentation

TABLE 4
Temnocyonine P4 Proportions (in mm)

	Measurement C[a]	Measurement D[b]	Ratio C/D
Temnocyon altigenis			
UCMP 9999	16.5	12.1	1.36
AMNH 6857	19.1	~12.6	—
USNM 7940	16.9	12.7	1.33
UCMP 1549	~17.8	~13.2	~1.35
Temnocyon subferox, new species			
YPM 10065	19.3	14.4	1.34
Temnocyon fingeruti, new species			
NM 280/61	22.0	15.4	1.43
Temnocyon ferox			
YPM-PU 10787	~22.2	16.5	~1.35
Mammacyon obtusidens			
ACM 34-41	25.2	21.5	1.17
LACM 5386	21.8	18.2	1.20
Mammacyon ferocior, new species			
F:AM 54134	26.0	23.1	1.13
Delotrochanter oryktes, new species			
ACM 4804	21.8	18.8	1.16
UNSM 47800	22.8	17.9	1.27
Delotrochanter major, new species			
F:AM 27561	23.5	19.8	1.19

[a]Length of the labial margin of P4.
[b]Greatest width of P4 measured transversely at the level of the protocone (fig. 47).

in the posterolingual cingulum of the *Mammacyon* m1 is also present at the same location on m2.

The m2 of *Delotrochanter* is known only in *D. oryktes* (only the anterior half of m2 survives in *D. major*) where it is elongated relative to m1 but not to the extent seen in *Mammacyon*. The m2 in species of *Temnocyon* is not elongate (table 6, ratio E/F), with values >1.67 for all but *T. macrogenys*; however, the range of values for *T. altigenis* itself suggests this is a variable trait. In *Rudiocyon*, m2 length is quite short relative to m1 length, demonstrating a marked difference from *Mammacyon*.

In summary, the temnocyonine genera are identified as follows: (1) *Temnocyon* (a paraphyletic taxon) retains the plesiomorphic dentition in which premolars are robust, tall, narrow, not reduced; m1 retains a tall trigonid with metaconid, a low talonid with enlarged hypoconid; m2 is short, not elongate relative to m1; P4–M1 are similar to the shearing carnassial pair in the dentally unspecialized amphicyonid *Daphoenus* (except that all teeth are proportionately larger in *Temnocyon*); (2) *Delotrochanter* has a derived durophagous dentition in which premolars (p2–4, P2–3) are short, robust, and posteriorly widened; the posterior accessory cusp (PAC) of p4 is centrally placed; m1 has lost the metaconid; the labial cingulum of m1 is straight, not sinuous; there is less height differential between m1 paraconid and hypoconid than in *Temnocyon*; m1 evolves a large centrally placed hypoconid in the terminal species, *D. oryktes* and *D. major*; m2 is slightly elongate in *D. oryktes*, the only species that preserves m2; in both *Delotrochanter* and *Mammacyon*, P4 has lost the typical form of a shearing carnassial and developed a short, rather blunt metastylar blade and an enlarged protocone for crushing occlusion, accompanying the lingual expansion of M1; P4 in *Delotrochan-*

TABLE 5
Measurements (in mm) Demonstrating Expansion of the M1 Protocone Region in Temnocyoninae

	Measurement A[a]	Measurement B[b]	Ratio A/B
Temnocyon altigenis			
UCMP 9999	13.8	8.3	1.66
AMNH 6857	14.0	~9.3	1.51
USNM 7940	13.8	9.0	1.53
UCMP 1549	~13.5	8.8	1.53
Temnocyon subferox, new species			
YPM 10065	14.7	10.2	1.44
Temnocyon fingeruti, new species			
NM 280/61	17.1	10.5	1.62
Temnocyon ferox			
YPM-PU 10787	18.2	12.1	1.50
Temnocyon percussor			
AMNH 81047	20.9	12.9	1.62
Mammacyon obtusidens			
ACM 34-41	20.4	15.5	1.32
LACM 5386	17.8	13.1	1.36
Mammacyon ferocior, new species			
F:AM 54134	21.4	17.4	1.23
Delotrochanter oryktes, new species			
ACM 4804	17.7	14.7	1.20
UNSM 47800	17.5	14.1	1.24
cf. *Delotrochanter*			
TRO 390	17.6	15.7	1.12

[a]Length of the labial margin of M1.
[b]Anteroposterior width of the M1 protocone region (fig. 46).

ter never attains the large size seen in *Mammacyon* despite the much younger geologic age of *D. oryktes* and *D. major*; (3) *Mammacyon* has a derived durophagous dentition in which premolars (p2–4) are elongate, narrow, with only p4 broadened posteriorly in *M. ferocior*; the p4 PAC is labially placed; m1 has lost the metaconid and the labial cingulum is sinuous; m1 shows less height differential between paraconid and hypoconid than in *Temnocyon*, and is similar in this respect to *Delotrochanter*. *Mammacyon* develops the longest m2 (relative to m1 length) of any temnocyonine. P4–M1 and m1–2 are massive crushing teeth with an enlarged, bulbous P4 protocone more developed than in *Delotrochanter*; (4) *Rudiocyon amplidens* is a large carnivore, possibly a sister taxon to *Mammacyon*; its m1 is the size of that in *D. oryktes* or *M. ferocior*; it has lost the m1 metaconid but differs from these species in retaining a narrow, laterally compressed p4 and short m2 lacking elongation.

SYSTEMATIC PALEONTOLOGY

CLASS MAMMALIA LINNAEUS, 1758
SUBCLASS THERIA PARKER AND HASWELL, 1897
INFRACLASS EUTHERIA GILL, 1872
ORDER CARNIVORA BOWDICH, 1821
INFRAORDER ARCTOIDEA FLOWER, 1869
FAMILY AMPHICYONIDAE HAECKEL, 1866
SUBFAMILY TEMNOCYONINAE HUNT, 1998: 207

Amphicyonid carnivorans in which the premolars (P2–3, p2–4) are particularly tall

TABLE 6
Temnocyonine Dental Ratios[a]

	Ratio A/B	Ratio C/D	m1 metaconid	Ratio E/F
TEMNOCYON				
altigenis	1.51–1.66	1.33–1.36	yes	1.67, 1.68,1.73, 1.83
subferox	1.44	1.34	?	—
fingeruti	1.62	1.43	yes	1.67
ferox	1.50	~1.35	yes	1.79
percussor	1.62	—	yes	1.69
macrogenys	—	—	yes	1.62
RUDIOCYON				
amplidens	—	—	no	1.89
DELOTROCHANTER				
petersoni	—	—	no	—
oryktes	1.20–1.24	1.16–1.27	no	1.69
major	—	1.19	no	~1.64
MAMMACYON				
cf. (LACM 15908)	—	—	vestigial	1.71
obtusidens	1.32–1.36	1.17–1.20	no	1.57
ferocior	1.23	1.13	no	1.60

[a]Ratios: **A** = greatest labial length of M1, **B** = anteroposterior width of M1 protocone region, **C** = greatest labial length of P4, **D** = greatest width of P4 measured transversely at the level of the protocone, **E** = m1 length, **F** = m2 length.

and well developed, and the carnassials and molars of several genera adopt a specialized crushing-shearing morphology unique among the Carnivora. In older individuals these premolars show strong apical wear similar to living bone-crushing hyaenids in which the principal cusps are worn to flat platforms by contact with hard materials. Such apical wear also can be observed on carnassials and molars. The carnassial pair remains functionally prominent throughout the history of the subfamily, and is always flanked by a large first and smaller second molar in the maxilla, and by a prominent m2 and small m3 in the mandible. Plesiomorphic species retain an m1 metaconid that is lost in derived forms. The talonid of the lower carnassial is occupied by an enlarged hypoconid cusp (there is no entoconid), followed in series by the m2 protoconid and hypoconid, forming a line of three strong, blunt, crushing cusps (there is a vestigial m2 metaconid in some species but never an entoconid). In the maxilla the M3 is always absent, a loss occurring in only a few other amphicyonid groups. M1 is diagnostic of the subfamily: its protocone becomes isolated on an enamel platform forming the lingual half of the tooth, and an enlarged lingual cingulum develops surrounding the protocone region. M2 is similar in form to M1 but is much reduced in size and also has an isolated protocone and developed lingual cingulum. The upper carnassial is as morphologically diagnostic as M1, especially in younger species: the P4 protocone is enlarged and lingually directed, becoming a bulbous crushing cusp, and in the more derived species a shortening of the metastylar blade accompanies the size increase of the P4 protocone.

Skull form differs among temnocyonines. The larger species of *Temnocyon* are characterized by dolichocephalic skulls, similar to the wolf skull, although with broader, shorter snouts. The only complete skull of *Mammacyon* displays proportions similar to living ursids, whereas the only skull of *Delotrochanter* reveals a short, deep hyenalike skull. In several species the frontal region of the skull is strongly inflated. As body size increases, the volume of the braincase fails to keep pace with skull size; consequently brain volume in the large terminal species does not equal that

TABLE 7
Cranial Dimensions (in mm) of Temnocyoninae

Taxon	Museum No.	Basilar length	Width, braincase	Width, frontal sinuses
Temnocyon altigenis	UCMP 9999	167	53	41
Temnocyon altigenis	UCMP 1549	180	55	46
Temnocyon subferox	YPM 10065	210	62	47
Temnocyon ferox	YPM-PU 10787	260	72	58
Temnocyon fingeruti	NM 280/61	250	64	64
Temnocyon macrogenys	F:AM 54139	300[a]	—	—
Mammacyon obtusidens	ACM 34-41	255	64	50[b]
Mammacyon ferocior	F:AM 54134	280	67	71
Delotrochanter oryktes	ACM 4804	250[a]	—	—
	UNSM 47800	245	80[c]	69[d]
Rudiocyon amplidens	LACM 480	—	65	—

[a]Estimated from mandibular length.
[b]Estimated width of damaged frontal region.
[c]Estimated by measuring from the midline of the skull to the braincase on one side and doubling the measurement.
[d]Estimated by measuring from the midline to the postorbital process on one side and doubling the measurement.
All measurements are approximate due to minor distortion and crushing of skulls.

seen in large living carnivorans of the same size (table 7). The skulls that preserve the basicranium display an embayed basioccipital and small plesiomorphic auditory bullae. An ossified entotympanic contribution to an ectotympanic bulla is confirmed in a single species, *Temnocyon fingeruti*, from the John Day Formation. However, no entotympanic inflation or enlargement occurs in these temnocyonines. Dental formula for the subfamily: 3-1-4-2/ 3-1-4-3.

Postcranial bones associated with a few crania and mandibles (table 8) indicate that the forelimbs and feet were often elongated, with the exception of the stem species *Temnocyon altigenis*. The forelimb was not everted at the elbow, as is common in the large amphicyonines (*Amphicyon*, *Ysengrinia*), but was held in a more erect vertical alignment. Species of *Mammacyon*, *Delotrochanter*, and *Temnocyon* were experimenting with a cursorial gait: longer limbs were becoming adapted for fore-aft parasagittal motion, and an erect stance accompanied paraxonic, digitigrade fore- and hind feet.

Temnocyon Cope, 1878

TYPE SPECIES: *Temnocyon altigenis* Cope, 1878.

INCLUDED SPECIES: *Temnocyon altigenis* Cope, 1878; *T. subferox*, new species; *T. ferox* Eyerman, 1896; *T. percussor* Cook, 1909; *T. fingeruti*, new species; *T. macrogenys*, new species.

DISTRIBUTION: Early Arikareean, Oregon and California; late Arikareean, Oregon and western Nebraska; latest Arikareean, southeastern Wyoming.

DIAGNOSIS: A paraphyletic genus distinguished from other temnocyonines by presence of a metaconid on m1; by plesiomorphic form and proportions of M1–2, m2 (with labially situated proto-and hypoconids), upper and lower carnassials, and premolars (P4–M1 ratios A/B, C/D, table 6). See tables 1–5.

DISCUSSION: The genus includes stem temnocyonines that preserve the plesiomorphic form of the cheek teeth, only slightly modified in the younger and larger derivative species of the genus. *T. subferox* apparently evolved from *T. altigenis*, the earliest and smallest temnocyonine species. Larger and more dentally derived *T. ferox*, *T. percussor*, and *T. fingeruti* retain a number of primitive dental features and represent larger species evolved from within the *T. altigenis–T. subferox* group. The enormous *T. macrogenys,* the last representative of the genus, is most likely derived from *T. percussor*. The genus ranges in time from the earliest to latest Arikareean.

TABLE 8
Dimensions of the Temnocyonine Postcranial Skeleton

Mus. no.	Humerus[a]	Radius	Ulna	MC	Femur	Tibia	MT	Ph (MC)
Temnocyon altigenis								
UCMP 9999	159	~132	~158		~175		II, 57.3	
Temnocyon ferox								
YPM-PU 10787	206	186	233	I, 37.4	244	222	I, 45.0	pI, 21.8
				II, 57.2			II, 69.7	pII, 29.4
				III, 71.0			III, 82.3	pIII, 30.8[b]
				IV, 71.6			IV, 84.3	pIV, 30.5[c]
				V, 49.8			V, 75.9[d]	pV, ~27
Mammacyon obtusidens								
ACM 34-41	217	~205	~227	II, 59.1		~239		
							III, 84.0	
							IV, 85.0	
							V, 69.8	
Mammacyon ferocior								
F:AM 27562	247	227[e]	287	II, 71.7	~275	265	II, 83.0	
							III, ~94	
Delotrochanter oryktes								
UNSM 47800							II, 74.1	
				III, 82.6			III, 90.9	
				IV, 83.9			IV, 91.0	
				V, 65.0			V, ~74[f]	
ACM 4804[g]	220	210	258	I, 40	246	228		
				II, 66			III, 89	
				V, 62			IV, 88	

[a]All measurements are lengths in mm (MC, metacarpal; MT, metatarsal; Ph, proximal phalanges of MC I–V).
[b]Intermediate phalanx, digit III, 18.9.
[c]Intermediate phalanx, digit IV, 19.2; ungual phalanx, digit IV, ~13.
[d]Intermediate phalanx, digit V, 15.2; ungual phalanx, digit V, 13.2.
[e]Calculated from complete ulna; radius absent.
[f]This metatarsal V was found in 1904–1905 by the Carnegie Museum and numbered CM 1589b but it is likely the same individual as UNSM 47800 from the Beardog Hill den.
[g]Measurements from Schlain (1980).

Temnocyon altigenis Cope, 1878
Figures 4–8, 65

Temnocyon altigenis Cope, 1878 (December 3): 6–8; 1879a: 68–70; 1879b: 55–69; 1881: 179; 1883: 238, figs. 2–3; 1884: 903–905, pl. 68, fig. 9, pl. 70, fig. 11.
Temnocyon altigenis: Merriam, 1906: 21–28, text figs. 7–11, pl. 3 (fig. 2).
non *Temnocyon altigenis*: Thorpe, 1922: 167–168; Hough, 1948: 100–101 (YPM 10065 is removed from *T. altigenis*).

TYPE: AMNH 6855, right mandible with p2–m2 and alveoli of the canine and p1, from the John Day beds, Oregon.

DISTRIBUTION: Early Arikareean, John Day Formation, Oregon.

DIAGNOSIS: Smallest and most plesiomorphic North American temnocyonine species distinguished from all other species of *Temnocyon* by small size and range of m1 lengths, 17.4–19.5 mm (table 2), and from *T. subferox*, *T. fingeruti*, and *T. percussor* by either M1 or P4 proportions (dental ratios A/B, C/D, table 6); from *T. ferox* and the huge *T. macrogenys* by much smaller size. Ratio of m1/m2 lengths, 1.67–1.83, indicating a short m2 relative to m1, thus distinct from species of *Mammacyon* (1.57, 1.61) but not

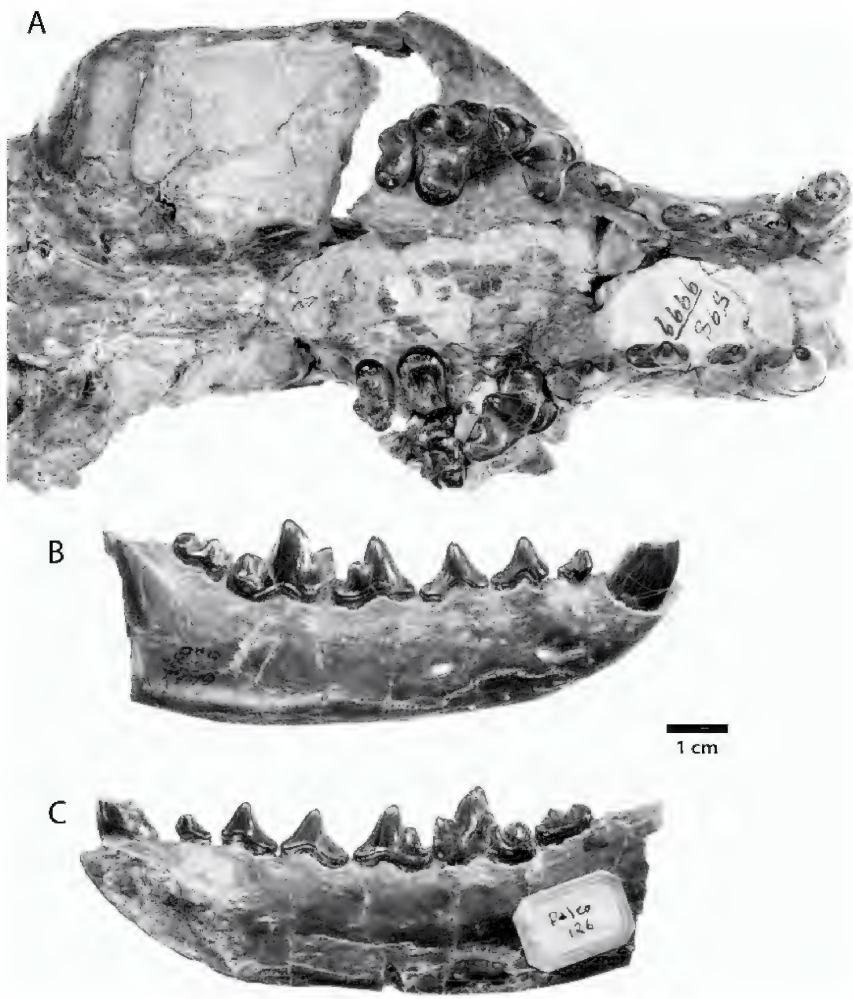


Fig. 4. *Temnocyon altigenis* (UCMP 9999) from Logan Butte, Crook Co., Oregon: **A,** palate with right C, P1–M2; **B, C,** right mandible with c, p1–m2 in labial and lingual views. Its skull, dentition, and small size establish UCMP 9999 as the most plesiomorphic temnocyonine.

from other *Temnocyon* species (ratios of 1.62–1.79) or *Delotrochanter* (1.64–1.69). Basilar length of skull, ~16–18 cm relative to 21–30 cm for other *Temnocyon* species (table 7); frontal sinuses moderately inflated.

REFERRED SPECIMENS: (1) AMNH 6856, left lower jaw with c, p2, p4–m2, alveoli of p1, p3, and m3, from the John Day beds, Turtle Cove, Grant County, Oregon; (2) AMNH 6857, right lower jaw with p2–m1, roots or alveoli of c, p1, m2–3, partial rostrum anterior to the orbits, with attached left lower jaw fragment, right C, P2–M2, alveolus of P1, left I3–C, P1–3, left c, p1–4, the entire left dentition highly fragmented, and a partial postcranial skeleton, from the John Day beds, Turtle Cove, Grant County, Oregon; (3) USNM 7940, left lower jaw with m1, m2 erupting, and damaged deciduous teeth; right maxilla with C, P1, P2–3 erupting, M1 fully erupted, P4 and M2 erupting, DP2–3, DC, from the John Day beds, Turtle Cove, Grant County, Oregon; (4) UCMP 1549, nearly complete uncrushed skull without basicranium, with right I1–2, alveolus for I3, C, P1–M2 (P4–M2 with parts missing); left I1–P1, P2 roots, P3–M2 (P4–M1 damaged), partial endocast of temporal lobes

Fig. 5. *Temnocyon altigenis* (UCMP 9999), John Day Formation, Logan Butte, Crook Co., Oregon.

exposed and undistorted, from John Day beds, Morgan's Place, UCMP loc. 874, Grant County, Oregon, collected by UCMP party, 1899; (5) UCMP 9999, skull with well-preserved basicranium, associated lower jaws, and much of the postcranial skeleton; teeth present include right C–M2, left C–P4, M2 (damaged M1); right C–M2 (broken M3); left C–M3; from the John Day beds, Logan Butte, Crook County, Oregon, collected by Davis and Osmont, 1900.

DESCRIPTION: The lower jaws of the hypodigm are very similar in dental morphology and size and can be described as a group (AMNH 6855, 6856, 6857, USNM 7940, UCMP 9999). In 1884 Cope described and figured AMNH 6855 and the rostrum of AMNH 6857; he briefly mentioned AMNH 6856 and the jaws of AMNH 6857. Although Merriam (1906) mentioned UCMP 1549, it has never been described or figured, but in this same paper considerable attention was given

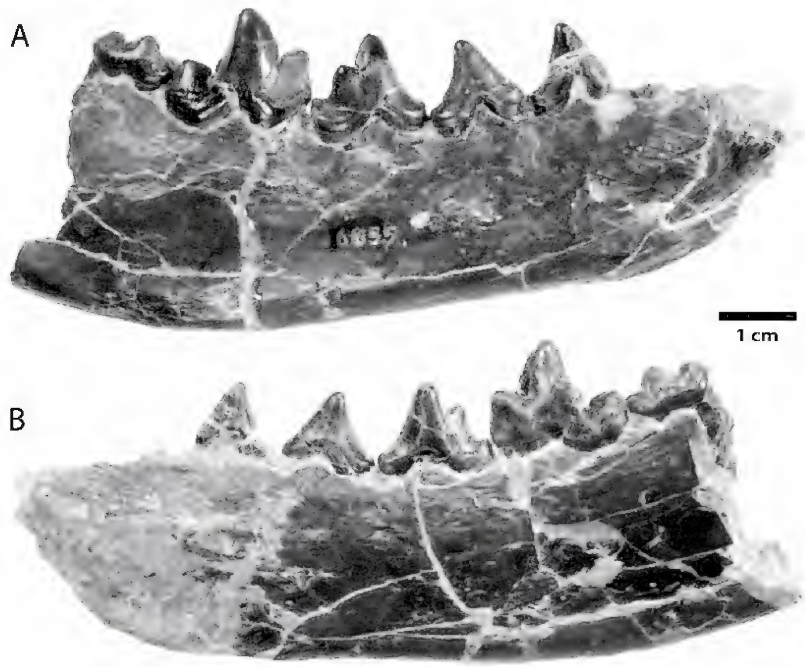


Fig. 6. Holotype of *Temnocyon altigenis* Cope (AMNH 6855), John Day Formation, Oregon. Right mandible with p2–4, m1–2 in (**A**) labial and (**B**) lingual views.

Fig. 7. *Temnocyon altigenis* (UCMP 1549), John Day Formation, Morgan's Place, UCMP loc. 874, near the town of Monument, Grant Co., Oregon. (**A**) lateral and (**B**) dorsal views of uncrushed cranium.

to the associated skull, jaws, and skeleton from Logan Butte (UCMP 9999), which is arguably the most plesiomorphic North American temnocyonine, based upon its dental traits.

The premolars of these lower jaws from the John Day beds are exceedingly similar in form and size: there is a progressive increase in size from p1–4, with p1 a rather small single-rooted tooth relative to p2–4. There are no accessory cusps with the exception of a prominent laterally placed posterior accessory cusp on p4, the plesiomorphic state for the subfamily. The premolars are not crowded except in young animals with newly erupting premolars. In adults the premolars are ranked in a linear series and are narrow with anterior and posterior slopes each traversed by a fine enamel ridge, running down each slope from the tip of the principal cusp to the base of the tooth. Only p4 shows any posterior expansion in width at the base of the tooth, and this is very slight (6.8 mm vs. 5.4 mm anterior width, AMNH 6855).

The molars are also similar in form and size within the hypodigm, with the exception of AMNH 6856, which has a short m2

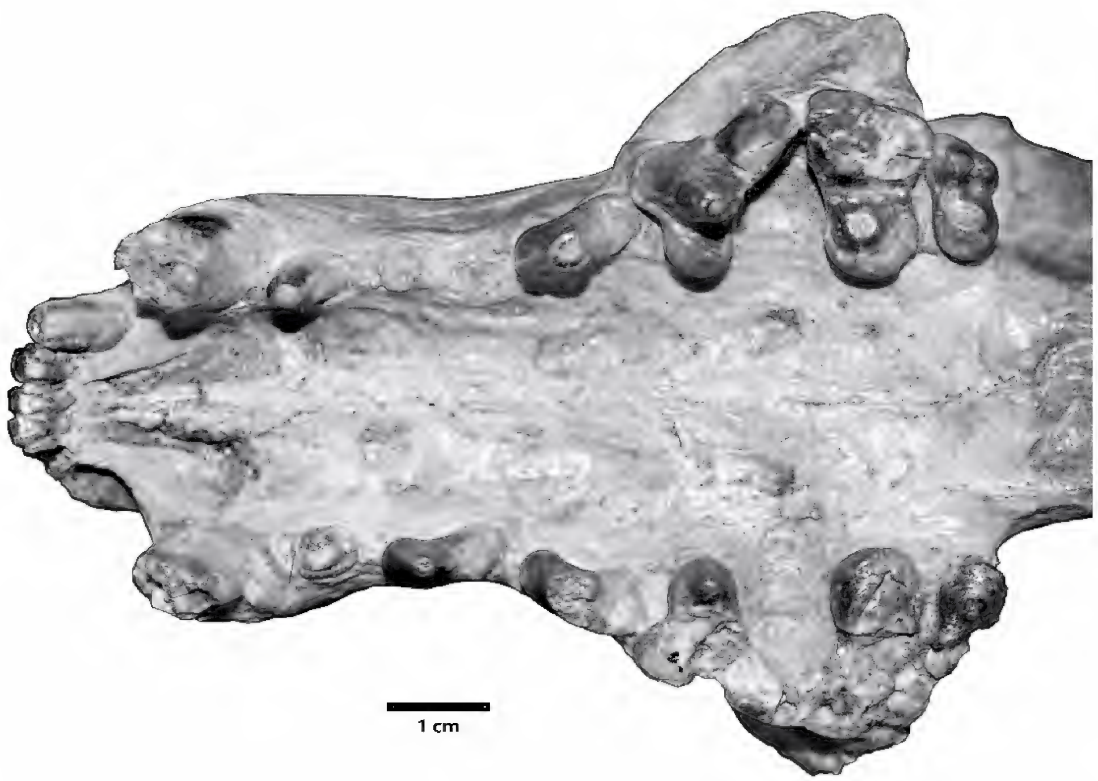


Fig. 8. Palate with I1–3, C, P1–4, M1–2 of *Temnocyon altigenis* (UCMP 1549), John Day Formation, Morgan's Place, UCMP loc. 874, near the town of Monument, Grant Co., Oregon.

relative to m1 length (table 6, ratio E/F, 1.83). All lower carnassials conform to a common pattern: the trigonid is high, the three principal cusps present but unequally developed—the tall protoconid is the main cusp, the paraconid and metaconid lower and at about the same height. The metaconid is somewhat reduced and is located both internal to and posterior to the protoconid. The paraconid forms a robust bladelike cusp anterointernally directed. The m1 talonid is short relative to the trigonid: it is much lower relative to the trigonid than in younger, larger species of temnocyonines in which the height inequity is resolved. The m1 talonid is dominated by a large, prominent, centrally placed hypoconid; there is no entoconid. The m2 is characterized by a trigonid somewhat longer than the talonid; there are two main cusps, the protoconid and hypoconid, situated one behind the other toward the labial edge of the tooth. The paraconid is small, occupying the anterointernal corner of m2. The m2 metaconid is absent or in USNM 7940, a juvenile with unworn teeth, a small vestigial metaconid is discernible; a low ridge extends from protoconid to the lingual edge of m2, and in all other specimens except USNM 7940 the ridge is uninterrupted by a metaconid cusp. The anterolabial corner of m2 is slightly protruded in some individuals (AMNH 6856).

The m3 is preserved only in UCMP 9999, where it is a very reduced version of m2. It is rectangular in occlusal outline, not circular. The protoconid and hypoconid are labially placed; there is a small paraconid.

Depth of the lower jaw below the m1 hypoconid (in mm) is: AMNH 6855, 30.7; AMNH 6856, 26.8; AMNH 6857, ~25.4; USNM 7940, 20.6 (juvenile); UCMP 9999, 23.3.

The rostrum described by Cope (1884: 904–905, pl. 70, fig. 11) is much less well preserved than his description implies. The

left upper and lower jaws are still in matrix and the teeth badly shattered so that preparation is unwarranted. The right upper dentition, which Cope figured, is so badly damaged that it would be useless for diagnosis were it not for the associated lower jaws. The only undamaged tooth is M2.

However, the intact upper teeth of UCMP 9999, described by Merriam (1906), can be used to supplement the description of Cope's rostrum. UCMP 9999 from Logan Butte has a gracile dentition relative to the Turtle Cove material, which forms the greater part of the *T. altigenis* hypodigm. UCMP 9999 may prove eventually to represent a somewhat older and more primitive species but is here considered a gracile female morph of *T. altigenis*.

The upper premolars of UCMP 9999 are without accessory cusps and were not as crowded nor as tall as the lower premolars. They are triangular, narrow teeth with a slight widening at the posterior base of P3. P4 is a shearing carnassial, although the protocone is enlarged, anticipating the marked change in P4 form that occurs in the younger, more derived temnocyonines. There is little to distinguish the *T. altigenis* P4 from that of *Daphoenus*, other than the more prominent protocone in the former. P4 is surrounded by a distinct basal cingulum, more defined lingually.

M1 is intact only in UCMP 9999 and USNM 7940 where it demonstrates the plesiomorphic temnocyonine pattern. Portions of M1 occur in UCMP 1549 and AMNH 6857 where they indicate a tooth of the same type. The protocone is low and anteriorly placed as in *Daphoenus*, not yet completely isolated on a broad enamel flat as in younger, more derived temnocyonines. The cingulum anterior to the protocone was not swollen as it is in more derived species, an indication that this carnivore retained a highly sectorial carnassial. However, temnocyonine hallmarks have already appeared: the lingual cingulum is slightly swollen, and the paracone and metacone are prominent with a developed parastylar region. Consequently, both the labial and lingual parts of M1 are enlarged, creating the impression that the tooth is somewhat constricted in its middle part in occlusal view. The protocone of M1 is connected by a preprotocrista to the anterior cingulum, a feature retained in most larger, derived species of the genus. A small paraconule is present on the preprotocrista. The postprotocrista is absent and there is no metaconule. The configuration of M1 in UCMP 9999 is the most plesiomorphic of any North American temnocyonine. From this pattern evolved the enormous crushing M1s of the more dentally derived Arikareean species of the subfamily.

M2 is much smaller than M1. Its metacone is more reduced, and its protocone is isolated on an enamel shelf surrounded by a thickened lingual cingulum. Length of the upper toothrow of AMNH 6857 from the anterior alveolar border of P1 to the posterior edge of M2 is 67.2 mm: crushing has to some extent altered the actual distance, but in UCMP 9999 where distortion is less, the same measurement is 67.3 mm. The only significant difference warranting mention between the rostrum of AMNH 6857 and UCMP 9999 is that the upper canine is larger and more robust in AMNH 6857, suggesting it is a male, and more slender and gracile in UCMP 9999, presumably a female.

The Logan Butte skull (UCMP 9999) preserves the basicranium in which the auditory region shows a deeply embayed basioccipital bone containing an enlarged inferior petrosal venous sinus that conforms to the amphicyonid pattern (see Basicranial Anatomy).

I refer to *T. altigenis* a well-preserved, undistorted skull (figs. 7, 8, UCMP 1549), lacking the basicranium, mentioned by Merriam (1906: 22–24, 29) but not figured. The skull was collected near the town of Monument during the 1899 University of California–Berkeley expedition to the John Day beds. Merriam considered this skull merely an uncrushed version of UCMP 9999 from Logan Butte; its large canines, broad rostrum, and inflated frontal region suggest that it represents an intact male cranium of the species.

In dorsal view UCMP 1549 is a robust skull, similar in overall form to the much larger skull of *Mammacyon ferocior* (F:AM 54134). The inflated frontals and expanded rostrum swollen around the large canines are believed to be male traits. The braincase of

UCMP 1549, measuring 55 mm in greatest width, is surmounted by a low sagittal crest whose height is undetermined (the occiput is missing). Skull width decreases to 35 mm at the postorbital constriction, its narrowest point, and the width of the expanded frontal sinuses at the level of the postorbital processes is 46 mm. Anterior to the frontal region and the orbits, the maxillae are shallowly depressed, but in front of these depressions the snout expands due to the swelling of the maxillary region around the large canine roots: width of rostrum at the base of the canine roots is 40.7 mm. Both zygomatic arches are lost as is the occipital region and basicranium posterior to the basisphenoid. The distance between the infraorbital foramen and the posterior opening of the alisphenoid canal measures 83.4 mm.

I1–3 are preserved on the left side. I2 is somewhat larger than I1, but I3 is considerably larger than I2. I1 and I2 are worn flat at their tips but I3 is grooved obliquely on the posteroexternal face by the lower canine. There is a diastema of 4–5 mm between I3 and the upper canine. Width at the base of I3 (6.1 mm) relative to the more gracile I3 (4.6 mm) of UCMP 9999 reflects the male-female dichotomy.

The canine is robust, its root causing inflation of the maxilla and consequently a widening of the rostrum. Only the canine root and a small segment of the base of each tooth is preserved, so wear grooves cannot be identified. The left canine measures 14.6 mm in anteroposterior length by 9.7 mm in width at the alveolar margin.

About 2 mm posterior to the canine is a small peglike unicuspid P1, measuring 5.8 in length, 4.0 mm in width at the base of the crown.

P2 measures 10.9 mm in length, 4.6 mm in greatest width. It is heavily worn on its posterior surface, is wider behind the main cusp than in front, and has no accessory cusps. The posterior slope is slightly more inclined than the anterior, and a fine enamel ridge runs down each slope.

P3 measures 12.8 mm in length, 5.9 mm in greatest width. It is expanded at its posterior base, has a posterior slope somewhat longer than the anterior, but because of wear it is not possible to decide if accessory cusps were present.

P4 measures 17.8 mm in length of the labial margin, 13.2 mm in greatest width. Although both upper carnassials are damaged, the form of the tooth is discernible, much like P4 of UCMP 9999, although the protocone is somewhat more enlarged than in UCMP 9999. Also, the P4 protocone of UCMP 1549 was somewhat more posteriorly situated relative to the protocone of UCMP 9999, although the difference is quite small. P4 remains a shearing tooth but its height and enlarged protocone foreshadow the change in P4 form that occurs in the more derived temnocyonines from younger rocks.

M1 is 13.5 mm in length, 18.7 mm in width, and is best preserved on the left side. Although the left M1 has a broken metacone, the tooth is nearly intact, whereas most of the right M1 is missing. M1 is worn, the tips of paracone and protocone beveled to flat surfaces. The paracone was larger than the metacone, and the labial portion of M1 bearing the paracone-metacone was elevated, with a developed parastylar region. As in UCMP 9999, the lingual faces of paracone and metacone form a shear surface that descends to an enamel platform forming the lingual half of the tooth. On this enamel flat is situated an apically worn protocone. A distinct ridge (preprotocrista) leads from the protocone to the anterior cingulum; there is no postprotocrista. The protocone region is widened but no more than in UCMP 9999; this expansion is the result of the swollen or thickened posterior and medial parts of the lingual cingulum surrounding the protocone region: there is no expansion of the tooth anterior to the protocone and an anterior cingulum of normal width is developed. Thus a tricuspid m1 trigonid with developed metaconid would be expected in the lower jaw and such a tooth occurs in UCMP 9999. Cope's holotype lower jaw (AMNH 6855) and AMNH 6856, both with an m1 metaconid, occlude well with this skull. A small cuspule on the posterior border of M1 may represent a vestigial metaconule.

M2 measures 8.4 mm in length, 12.0 mm in greatest width. M2 is a small replica of M1 except that the protocone is more centrally located within the enamel flat forming the

lingual half of the tooth. The paracone is slightly larger than the metacone. No conules seem to be present but the tooth is well worn. The protocone was apparently a prominent knoblike cusp, which has been worn to a flat surface; it was surrounded by a slightly swollen lingual cingulum. As in UCMP 9999, the M2 is situated on a plane slightly above M1 in order to occlude with the m2, which was elevated and tilted forward on the ascending ramus of the mandible.

No M3 was present. M2 is the most posterior tooth in the maxilla and there is no space available for an M3.

The orbital region of the skull is intact and is characterized by a deeply excavated trough, which in its posterior part contains the sphenorbital fissure and the anterior foramen for the alisphenoid canal (the foramen rotundum in the beardog opens internally into the alisphenoid canal as in *Ursus* and *Canis*, hence cannot be seen). They are placed almost side-by-side where they perforate the sidewall of the skull, similar to their location in *Ursus*. Dorsal and anterior to this is a smaller optic foramen that also lies within the elliptical depression that includes the sphenorbital fissure and foramen for the alisphenoid canal. Leading directly forward beneath the optic foramen is a low horizontal ridge which extends craniad ~35 mm to end directly above the sphenopalatine foramina. This ridge probably marks the dorsal extent of the pterygoid musculature and corresponds closely to the palatine-orbitosphenoid suture. A second ridge runs upward at a 45° angle to the first, beginning above the sphenorbital fissure and coursing anterodorsad above the optic foramen. It forms the dorsal border of the elliptical depression housing these orbital foramina and terminates ~18 mm below the postorbital process. This same arrangement of ridges and foramina occurs throughout the Temnocyoninae and is evident in F:AM 54134 (*Mammacyon ferocior*) and YPM 10065 (*Temnocyon subferox*), and is suggested in YPM-PU 10787 (*T. ferox*) in which the orbital region is badly crushed.

Structure in the vicinity of the foramen ovale is similar in other members of the subfamily. The foramen ovale and posterior opening of the alisphenoid canal are contained in a deep common fossa. Anterior to this fossa is a shallow depression for pterygoid musculature, which is even more pronounced in *T. subferox* (YPM 10065) and *Mammacyon* (ACM 34–41, F:AM 54134). Medial to the common fossa for the foramen ovale and alisphenoid canal is an oval percussion fracture in the sphenoid bone, evidence that the missing basicranium may have been lost to a scavenger. Lateral to the foramen ovale is a remnant of the glenoid fossa. Little can be inferred about the middle ear cavity and surrounding basicranial structures other than that the anterointernal corner of the auditory region was deep, suggesting the presence of an auditory bulla similar to that known in *Temnocyon* (YPM 10065) and *Mammacyon* (ACM 34–41).

The skull of UCMP 1549 measures 146.5 mm in length from a point between the first incisors to the posterior border of the foramen ovale. The approximate distance between the same points on UCMP 9999 is ~130 mm. Basilar skull length of UCMP 9999 is ~167 mm. Assuming similar proportions for UCMP 1549, basilar length would be ~180 mm.

The rostrum of a juvenile animal (USNM 7940) from the John Day beds collected by William Day in 1883 includes part of the deciduous (DP2–3, DC) and permanent (P1, P4–M2 erupted) dentition. This animal agrees most closely with UCMP 1549 in the form of its P4–M1. P4–M1 are somewhat less sectorial than these teeth in UCMP 9999. This is evident in the more expanded protocone region of M1 and in the larger P4 protocone of USNM 7940. The unworn condition of these newly erupted teeth shows that initially the upper carnassial of *T. altigenis* had a modest cingulum entirely surrounding the tooth that was only weakly developed on the lingual face of the protocone. M1 is encircled by a cingulum as well, which is most pronounced posterolingual to the protocone and on the posterior face of the tooth but remains thin on the anterior face (as in UCMP 9999 and 1549). This condition of the cingulum clearly represents the plesiomorphic state prior to massive enlargement of the lingual cingulum in younger, larger temnocyonines.

DISCUSSION: *Temnocyon altigenis* Cope is the most dentally plesiomorphic species of

North American temnocyonines, and also the smallest in body size. The hypodigm was collected from the John Day beds of Oregon; none are known from the Great Plains or elsewhere in North America. Skulls attributable to the hypodigm indicate carnivorans with basilar lengths of ~16 to 18 cm (table 7).

The dentition of *T. altigenis* shares similarities with the teeth of the late Eocene-Oligocene amphicyonid *Daphoenus*. The principal differences are: (a) *T. altigenis* has all teeth larger than those of *Daphoenus vetus* of Orellan age despite similar skull size; (b) *T. altigenis* has taller premolars than *Daphoenus* (excluding P1/p1); (c) the *T. altigenis* P4 is larger and has a more robust lingually extended protocone relative to Orellan *Daphoenus*; (d) M1–2 of *T. altigenis* have expanded or swollen lingual cingula not found in *Daphoenus*; (e) *T. altigenis* has lost M3 which *Daphoenus* retains; (f) lower molars of *T. altigenis* lack entoconids, and have an enlarged m1 hypoconid and only an m2 protoconid and hypoconid relative to *Daphoenus*, which has a plesiomorphic amphicyonid m1–2; (g) *T. altigenis* has lost the m2 metaconid that *Daphoenus* retains.

Merriam's (1906) associated skull, mandibles, and partial postcranial skeleton from Logan Butte (UCMP 9999), is here interpreted as a small female of the *T. altigenis* hypodigm. The gracile canines, less swollen snout, less expanded frontal region, and smaller overall skull size are believed to indicate the female morph. Logan Butte is an isolated John Day outlier far distant southwest of Turtle Cove where most other *T. altigenis* fossils were found. Eventually UCMP 9999 may prove a distinct species—the most plesiomorphic North American temnocyonine—but for the present it is placed within *T. altigenis* as its teeth and dental measurements do not merit separation.

Temnocyon altigenis from the John Day beds shares some dental characteristics with European haplocyonine amphicyonids from the Aquitanian Allier Basin localities of St-Gérand, France. A holotype mandible of *Haplocyon elegans* (MNHN-SG 395: Bonis, 1966: pl. 3, fig. 4; Viret, 1929: pl. 8, fig. 1) displays teeth and dental measurements much like those of the Logan Butte jaw of *T. altigenis* (UCMP 9999). The holotype of *Haplocyon crucians* (MNHN-SG 404: Viret, 1929: pl. 8, fig. 2), a partial ramus with p2–4, and an m1 (MNHN-SG 403) are comparable to Cope's holotype of *T. altigenis* (AMNH 6855). This similarity between haplocyonine and temnocyonine dentitions had been previously noted by Viret (1929) and Bonis (1973).

In 1992 I was able to study Aquitanian haplocyonines in Paris through the courtesy of L. de Bonis and L. Ginsburg. Of all haplocyonines, *Haplocyon elegans* and *H. crucians* from St-Gérand are dentally closest to John Day *T. altigenis*, which is the most plesiomorphic North American species. However, subtle yet evident dental differences distinguish the St-Gérand forms from John Day *T. altigenis*—although similar in mandibular length, depth and tooth size, *H. elegans* (MNHN-SG 395) is dentally more plesiomorphic than UCMP 9999: (1) its m1 metaconid is not as reduced as in UCMP 9999; (2) the more plesiomorphic m2 trigonid is taller and wider, with fully developed metaconid, a low talonid with labially placed hypoconid, and an internal talonid shelf. In UCMP 9999 there is no m2 metaconid, the talonid is nearly equal in height to the trigonid, and the hypoconid nearly fills the talonid, which is not the case in MNHN-SG 395. In all the dental features where UCMP 9999 is more derived than MNHN-SG 395, the small Logan Butte carnivore closely approaches Cope's larger holotype of *T. altigenis* (AMNH 6855), suggesting a plausible male-female relationship between the two John Day fossils.

Finally, the age of the derived Logan Butte *Temnocyon altigenis*, found in proximity to tuffs dating from ~28.8–29.3 Ma, seems in conflict with the probable younger age (within MP29-MN2: ~26–20.5 Ma) of the more plesiomorphic *Haplocyon elegans* jaw from the St-Gérand basin.

Temnocyon subferox, new species
Figures 9, 10, 66

Temnocyon altigenis: Thorpe, 1922: 167–168.
Temnocyon altigenis (in part): Hough, 1948: 100–101.

TYPE: YPM 10065, nearly complete skull with basicranium but lacking the rostrum

Fig. 9. *Temnocyon subferox* (YPM 10065), John Day Formation, Oregon. Holotype cranium in (**A**) lateral and (**B**) high lateral oblique views. Rostrum restored to the left of dashed line.

anterior to P3; from the John Day Formation, John Day River, Oregon (a catalog entry at the Peabody Museum, Yale University, reads "Middle John Day"); teeth present include right P3–M2, left P4–M2. Collector or date of collection unknown, but cataloged in 1914.

DISTRIBUTION: Earlier Arikareean, John Day Formation, Oregon.

ETYMOLOGY: From the Latin, *sub*, for "less than, under" and *ferox*, "fierce," in the belief that the species precedes *Temnocyon ferox*.

DIAGNOSIS: Cranium and teeth intermediate in size (basilar length, ~21 cm) between *T. altigenis* (UCMP 9999, 1549, basilar lengths ~16–18 cm) and *T. ferox* (YPM-PU 10787, basilar length, ~26 cm) and without strong inflation of the frontal region (table 7). Differs from other species of *Temnocyon* (except *T. altigenis*) by (a) smaller size and more plesiomorphic P4–M2 in which a marked expansion of M1 protocone region has not occurred (ratio A/B, 1.44, table 6); (b) P4 sectorial with protocone placed in advance of paracone (more dentally derived species of *Temnocyon* have protocone directly lingual to paracone). No preprotocrista on M1 (present in *T. altigenis*). Retains most plesiomorphic auditory bulla of any known temnocyonine (see discussion of Basicranial Anatomy).

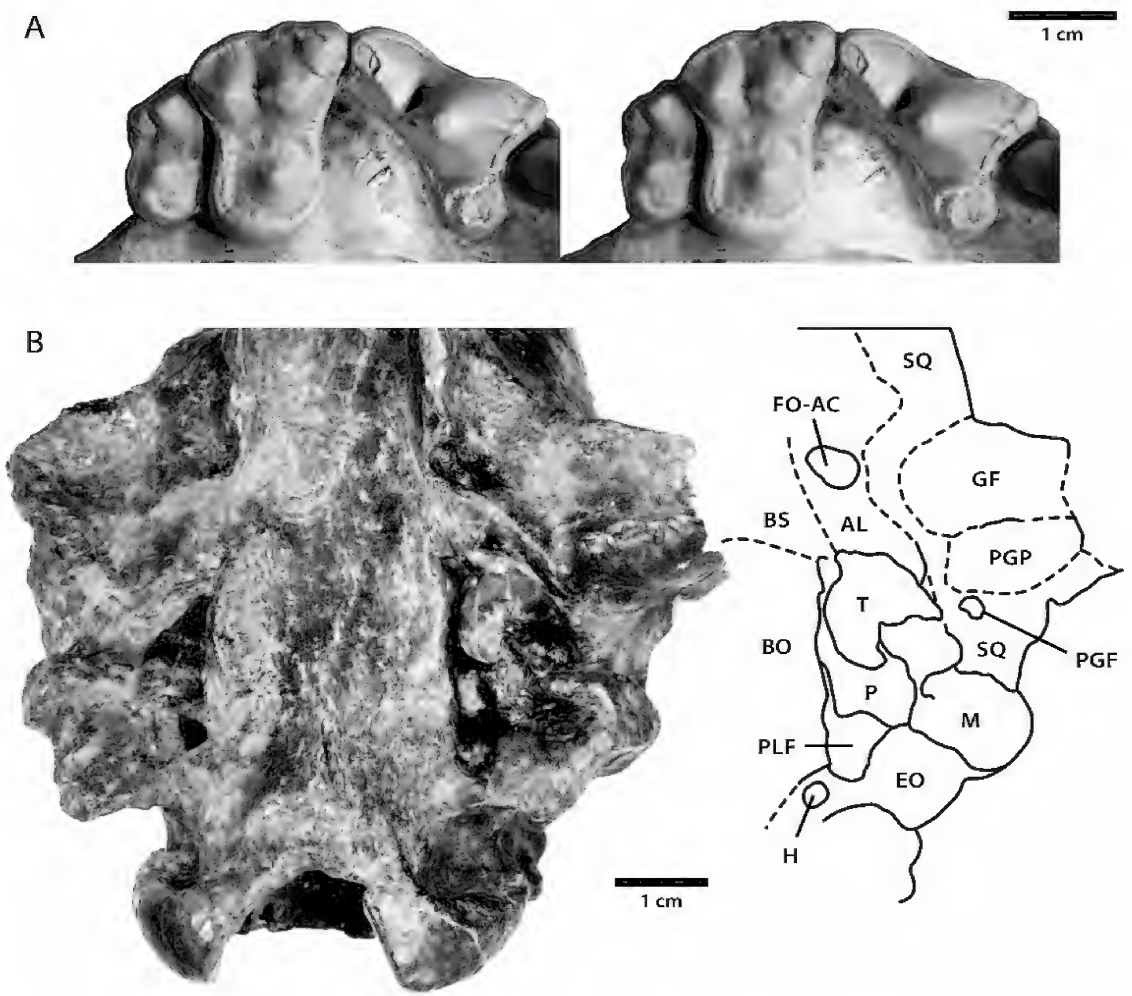


Fig. 10. Holotype of *Temnocyon subferox* (YPM 10065), John Day Formation, Oregon. **A,** maxilla with P4–M2; **B,** basicranium with remnant of ectotympanic bulla (stereopairs with negatives reversed). See figs. 66, 69. For abbreviations, see p. 5.

REFERRED SPECIMENS: None.

DESCRIPTION: The skull was first mentioned and briefly described by Thorpe (1922) in a discussion of doglike canids and amphicyonids in the Marsh collection at Yale. Later, Hough (1948: 101—"a specimen in the Peabody Museum, Yale University") mentioned the auditory region and recognized the presence of a remnant of the auditory bulla (she does not cite a catalog number but her description can apply only to YPM 10065). Neither Hough nor Thorpe illustrated the skull. The basicranium shows the deeply embayed basioccipital bone typical of amphicyonids, thought to contain an enlarged inferior petrosal venous sinus. The auditory region is reviewed and illustrated in the section on Basicranial Anatomy.

Although the skull is uncrushed and its form intact, the bone itself is fractured and altered by diagenesis after burial so that anatomical detail is lacking. The dolichocephalic skull has a gracile appearance with slender zygomatic arches and a long postorbital distance (orbital margin to occpital condyle is 14.3 cm). The frontal region is not inflated, thus similar to *T. ferox*, contrasting with the expanded frontal region of *T. fingeruti.* As in *T. altigenis*, the maxilla is slightly depressed above the prominent

infraorbital foramen. Foramina of the orbital region are as described for *T. altigenis*: an optic foramen, sphenorbital fissure, and anterior foramen for the alisphenoid canal open into the elongate depression that begins 18 mm anterior to the foramen ovale. The posterior opening of the canal and the foramen ovale share a common fossa. As in UCMP 1549 the foramen rotundum must open internally into the enclosed alisphenoid canal. Despite the loss of the rostrum the palate is preserved from P3 to M2; the cheek teeth seem quite small given the palatal area and skull size (greatest palatal width at P4–M1 is 6.5 cm; P4–M2 occupy 58% of this width). The mandibles must have been long and slender because of the modest glenoid fossa for a rather small narrow condyle, the small cheek teeth, and the considerable distance (~9 cm) from the glenoid fossa to the carnassial.

The left P4–M2 and right P3 survive whereas P1–2, incisors, and canines did not.

P3 is laterally compressed, slightly expanded posteriorly, and is taller than in *T. altigenis* and *T. ferox*. A fine enamel ridge runs from the principal cusp down the posterior slope to the basal cusp, the latter more prominent than a tiny posterior accessory cusp 2 mm anterior to the basal cusp. There are weak labial and lingual cingula that meet posteriorly to form the prominent basal cusp. P3 length, 12.9 mm; greatest posterior width, 6.6 mm.

P4 has a well-developed protocone, a sectorial paracone/metastylar blade, and is clearly a shearing carnassial. The metastylar blade is placed at a 45° angle to the anteroposteriorly aligned paracone. Length of the blade, 8 mm; paracone length, 10.3 mm. The protocone, lingual and slightly anterior to the paracone, is enlarged as is the protocone of *T. altigenis*. In *T. subferox* there is a broad embrasure between P4 and M1 into which the shearing m1 trigonid fits during carnassial occlusion. Dimensions of this embrasure in *T. subferox* are similar to those in *T. altigenis* (UCMP 9999) and represent the plesiomorphic state. Closure of this shearing embrasure between P4 and M1 occurs in the large species of *Mammacyon* and *Delotrochanter* where crushing takes precedence over shear.

P4 is encircled by a cingulum that is pronounced at the labial base of the metastylar blade. The cingulum is swollen at the anterolabial corner to form a parastyle, situated 2 mm anterolabial of the base of the enamel ridge descending the anterior face of the paracone. The protocone is a blunt knoblike cusp separated by a valley from the paracone and would have occluded with the heel of p4.

M1 is similar to the *T. altigenis* M1 except that the protocone region is more derived. A well-developed parastyle contacts the P4 metastylar blade. The labial cingulum is thickest at the parastylar region and thins posteriorly yet is still well defined along the entire labial margin of M1. The paracone is somewhat larger than the metacone. The internal faces of paracone-metacone form a vertical shearing surface that descends steeply to an enamel flat forming the lingual half of the tooth. A knoblike protocone is isolated on this enamel flat: no preprotocrista runs from the protocone across the enamel flat to the anterior cingulum as in the more plesiomorphic *T. altigenis*. This differs from *T. ferox* (YPM-PU 10787) that retains not only a pre- but also a weak postprotocrista.

The knoblike M1 protocone and its enamel flat are surrounded by a prominent cingulum, strongly thickened on the lingual margin, slightly less developed on the posterior margin, and thin but distinct anteriorly. Development of a swollen anterolingual M1 cingulum in temnocyonines accompanies loss of the m1 metaconid during closure of the embrasure between P4 and M1. There is no metaconule; a paraconule may be represented by a small cingular cusp on the anterior edge of M1 midway between protocone and paracone.

M2 is much smaller than M1 but remains a fully functional quadrate tooth with a weak parastyle. The paracone and metacone are elevated as in M1 but here the metacone is much smaller than the paracone. The lingual half of the tooth is a low enamel platform with a low blunt protocone. The tooth is surrounded by a prominent cingulum, lingually thickened as in M1.

M3 was not present in life: the maxillary border is smooth and unbroken posterior to M2, and there is no evidence of alveoli or roots for M3.

DISCUSSION: The skull, which is of considerable importance because of the basicranium, has been long ignored except for Hough's (1948) brief mention of its auditory region. It was first described by Thorpe (1922), who placed it in *T. altigenis*. However, the skull is much larger than the known crania of *T. altigenis* (UCMP 9999, 1549) and exceeds any reasonable upper limit of skull size predicted for the *T. altigenis* sample from the John Day region. Unfortunately, Yale University collection records for the skull do not establish an exact location, a collector, or a date of collection, only that it was cataloged in 1914 as YPM 10065, and that it may have come from the "Middle John Day." Whether the skull was found by collectors employed by O.C. Marsh in the late 19th century is unknown but is a possibility. It is surprising that such a well-preserved and unusual carnivore did not merit a more detailed description of its site of collection, which suggests it was found during one of the early Yale expeditions when exact locality data were rarely obtained. The stage of evolution of the skull relative to other North American temnocyonines indicates that a late Arikareean assignment is unlikely. An earlier Arikareean age is most probable, postdating the *T. altigenis* hypodigm in the John Day Formation.

The plesiomorphic dentition and weakly inflated frontal region of the skull make it a possible predecessor to *T. ferox* (YPM-PU 10787) from the "upper John Day beds." The lack of pre- and postprotocristae on M1 in YPM 10065, and their presence in *T. ferox*, seem to conflict with this view. However, with acquisition of larger samples, protocristae may prove to be variable features on the molars of these carnivorans. The morphological "distance" between *T. subferox* and *T. ferox* is greater than between skulls of *T. subferox* and *T. altigenis*, suggesting that substantial time intervened between YPM 10065 and *T. ferox*.

The skull of YPM 10065 is important to the determination of the broader relationships of temnocyonines since the basicranium and auditory bulla are preserved and largely undistorted. The bulla of *T. subferox* represents the most plesiomorphic condition found among temnocyonines. The auditory bulla in North American temnocyonines is known only in *T. subferox* (YPM 10065), in *T. fingeruti* (NM 280/61), and in *Mammacyon obtusidens* (ACM 34–41). These bullae are more fully discussed in the section on Basicranial Anatomy.

No mandible was associated with the skull of *T. subferox* (YPM 10065), and no isolated jaws from the John Day beds occlude satisfactorily, but there are two mandibles of North American temnocyonines that correspond in size: (a) LACM 15908, a partial mandible from the Sharps Formation of South Dakota; (b) LACM 470, a crushed mandible from Kew Quarry, Sespe Formation, Las Posas Hills, California.

The Sharps mandible (LACM 15908) is unlikely to belong to the same species as the holotype skull despite the size correspondence: the m2 protoconid and hypoconid are placed in the center of the tooth, not on the labial margin as in *Temnocyon*. The m1 metaconid of the Sharps jaw is reduced, more than expected for an m1 that would occlude with the shearing P4 of the holotype skull. This jaw likely represents an early member of the *Mammacyon* lineage. On the other hand, the Kew Quarry jaw includes a tall p3–p4 that corresponds to the tall P3 in YPM 10065. Here the Kew Quarry mandible is referred to *T.* cf. *T. subferox* pending discovery of associated upper and lower dentitions of the John Day species.

Temnocyon cf. *T. subferox*
Figure 11

Temnocyon cf. *T. altigenis*: Stock, 1933b: 35–37, pl. 1, fig. 6.

REFERRED SPECIMEN: LACM 470, right mandible with c, single-rooted p1 alveolus, alveoli of p2, damaged p3–m2, including anterior part of ascending ramus, from Kew Quarry, Las Posas Hills, CIT loc. 126, Sespe Formation, Ventura County, California, collected by Thurston, 1930, early Arikareean.

DESCRIPTION: The crushed and fragmented lower jaw was accurately described and figured by Stock (1933b: 35–37). Premolars are closely spaced but not crowded, and p3–4 are tall, more so than in *T. altigenis*. The m1 is larger than any *T. altigenis* carnassial (table 2): both trigonid and talonid are

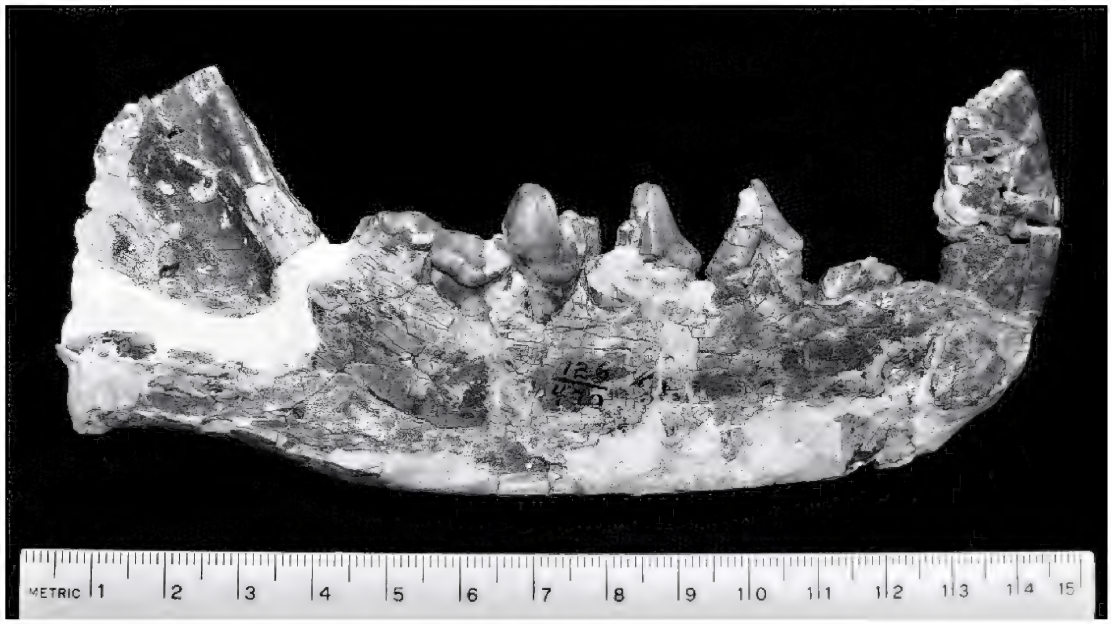


Fig. 11. *Temnocyon* cf. *T. subferox* (LACM 470), right mandible with p3–m2, damaged c, p1–2, from Kew Quarry, Sespe Formation, Ventura Co., California. This is the only record of the subfamily in western North America other than fossils from the John Day region.

broadened relative to *T. altigenis*. The m1/m2 length ratio is estimated at ~1.8, similar to *T. ferox*, taking into account damage to both molars—there is a relatively short plesiomorphic m2. The preserved lower teeth (p3–m2) are all slightly wider and more robust than these teeth in *T. altigenis* (table 2). The mandible is only 25 mm in depth below the hypoconid of m1, its width much compressed by crushing.

Discussion: The Kew Quarry mandible from the Sespe Formation displays differences in size and proportion of the posterior premolars and molars that argue against its placement in *T. altigenis*. The upper teeth of *Temnocyon subferox* (YPM 10065) satisfactorily occlude with the teeth of the Kew Quarry jaw, and indicate a carnivore of approximately the same size. However, there is no associated mandible with the holotype skull of *T. subferox* (YPM 10065) nor is there any other mandible of appropriate size from the John Day beds that can be referred to the skull. The dentary itself is not diagnostic but is quite shallow as would be predicted for *T. subferox*.

An important contrast exists between the Kew Quarry mandible and the holotype mandible of *Delotrochanter petersoni* n. sp. (CM 1603). CM 1603 belonged to a carnivore only slightly larger than the Kew Quarry animal, yet its p2 is short, with a large posterior and a small anterior root, placed very close together. The Kew Quarry p2 is elongate, and its two roots are of about equal size and spaced well apart. Thus the Kew Quarry carnivore does not approach *Delotrochanter* in premolar form, since the p2 is a key derived trait of the latter genus, nor does its m1 show the straight (as opposed to sinuous) labial cingulum found in *Delotrochanter*. The Kew Quarry animal cannot be referred to *Mammacyon* because it lacks shared derived dental traits of that genus: the notched lingual margin of the m1 talonid and the elongate m2. It is more likely that the Kew Quarry mandible belongs to a carnivoran similar to the John Day *Temnocyon subferox* that retained the shearing dentition typical of the *Temnocyon* lineage. Fossil mammals found with LACM 470 in Kew Quarry favor an early Arikareean age for the

quarry assemblage (see discussion in Age and Correlation).

Temnocyon ferox Eyerman, 1896
Figures 12–14, 53

Temnocyon ferox Eyerman, 1896: 268–284, pl. 11, figs. 1–9.
Temnocyon ferox: Wortman and Matthew, 1899: 115–118, fig. 3.
Temnocyon ferox: Merriam, 1906: 22–23, 29.

TYPE: PU 10787, as given in Eyerman (1896), a nearly complete articulated skeleton with associated skull and lower jaws, the basicranium badly damaged. Found in the same block with a partial oreodont skeleton, "near Maginnis' ranch, Turtle Cove, John Day river, Upper John Day beds, Oregon," collected by L.S. Davis, 1889. The type is now conserved in the Yale Peabody Museum collection and is numbered YPM-PU 10787.

DISTRIBUTION: Mid- or late Arikareean, John Day Formation, John Day valley, Oregon.

DIAGNOSIS: Wolf-sized species of *Temnocyon* (basilar skull length, ~26 cm), distinguished from *T. altigenis* and *T. subferox* by much larger size, from *T. macrogenys* by much smaller size, and from the *Mammacyon obtusidens–M. ferocior* group by retention of the m1 metaconid and possession of a short m2 relative to m1 (ratio E/F, ~1.6 in *Mammacyon*; ~1.8 in *T. ferox*). *T. percussor* is distinguished from *T. ferox* by its taller, broader p3–4 and by its larger more robust m1–2 and M1 (tables 2, 3). *T. ferox* and *T. percussor* share a similar m1–2 form but *T. percussor* represents a larger species. *T. fingeruti* differs from *T. ferox* in its more elongate, narrower m1, longer m2, disproportionate size of M1–2 (small M2 relative to M1 in *T. ferox*; large M2 in *T. fingeruti*); dental ratios (table 6); and more inflated frontal region.

REFERRED SPECIMENS: None.

DESCRIPTION: Eyerman described and figured the type specimen of *T. ferox* (1896: 268–279, pl. 11), reporting that it came from the upper John Day beds, Turtle Cove, Oregon, and so I include here only relevant observations to facilitate comparison with other temnocyonine species of similar size.

The skull and associated mandibles are crushed and fragmented, held together by an extremely hard, indurated gray tuff that preserved the articulated skeleton. Sutures and other fine anatomical details are obscured and distorted. The skull has a basilar length of ~26 cm. The snout is of moderate length: preorbital distance, ~10 cm; postorbital ~16 cm. Relative to *Canis lupus* the preorbital distance is proportionately shorter and the postorbital longer. The frontals are little inflated, much less so than in *T. fingeruti*, a carnivore of about the same size. The basicranium unfortunately is so damaged that no details can be identified.

The dentition reflects the plesiomorphic pattern seen in *T. altigenis* and *T. subferox*, is simply scaled to larger size, differing most notably in the form of M1–2. The p1 is represented by a single alveolus; p2 and p3 are not robust as in *Mammacyon* and *Delotrochanter* but rather low as seen in *T. altigenis* from Logan Butte—they carry no posterior accessory cusps and have thin enamel ridges traversing their anterior and posterior faces; p4 is distinctly larger than p3 and has a labially placed posterior accessory cusp—p4 has a squared heel with a centrally placed cingulum cusp and is elongate relative to m1 length. The m1 is a short, rather broad carnassial retaining a slightly reduced metaconid; the m1 talonid is nearly entirely occupied by the massive hypoconid (there is no entoconid); the hypoconid is much lower in height than the m1 paraconid. The m2 is short, a striking feature of the species; m1/m2 length ratio is ~1.8. The m2 trigonid is dominated by a large protoconid and the talonid by a hypoconid, both labially placed—there is no metaconid and only an extremely reduced paraconid; the trigonid width is 8 mm, and the talonid narrows to a width of 6.6 mm. The m1 hypoconid and m2 protoconid-hypoconid form a linear series of three blunt, crushing cusps.

The upper premolars are also low-crowned, gradually increasing in height from P1–3. Only P3 has a posterior accessory cusp, very small, somewhat labial in position above a slightly expanded heel with a squared posterior border. Although the upper carnassials are damaged, the metastylar blade was apparently short and the protocone modestly enlarged. M1 still retained a parastyle, and a prominent cingulum surrounded

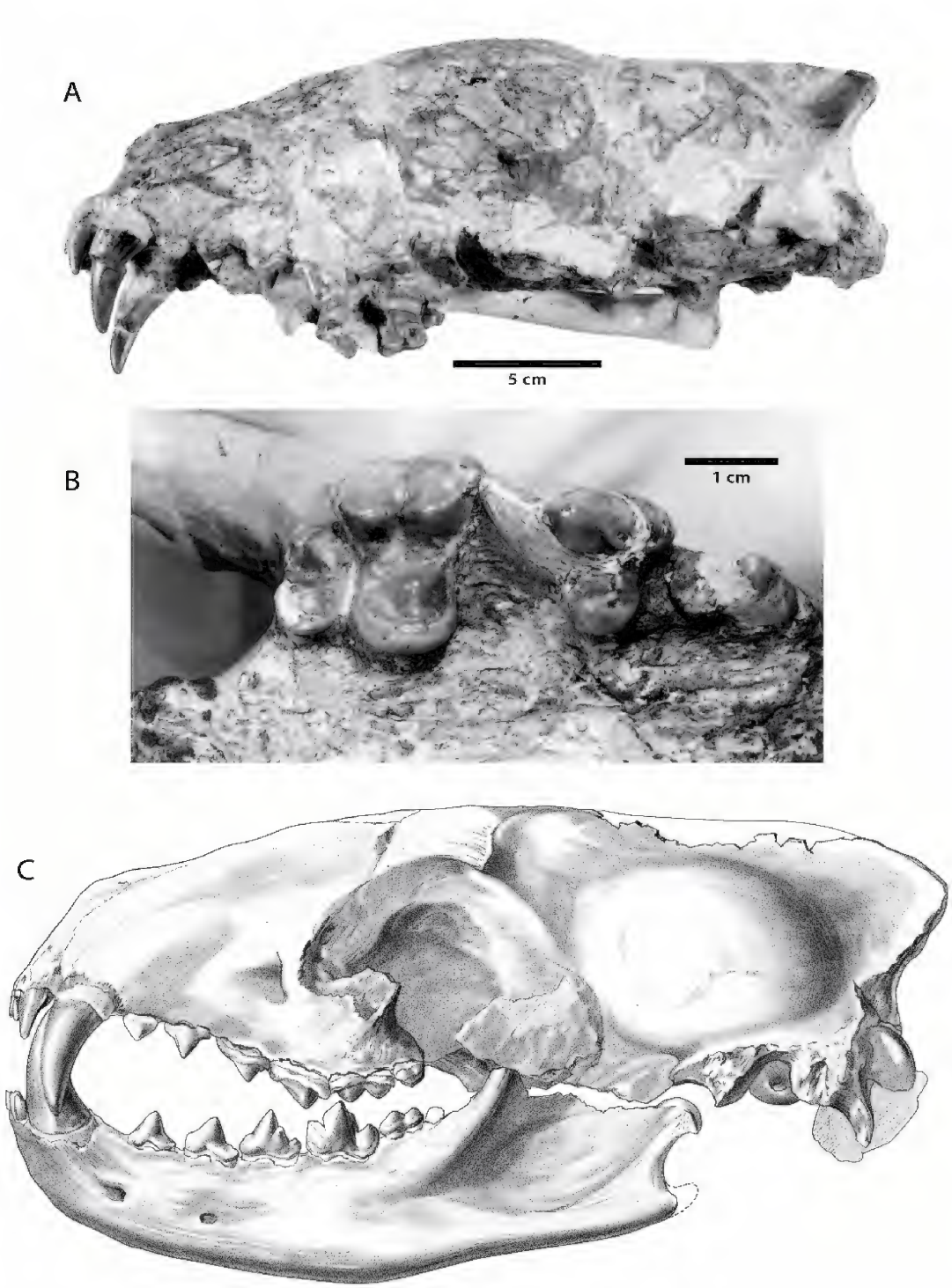


Fig. 12. Holotype of *Temnocyon ferox* Eyerman (YPM-PU 10787), from "near Maginnis' ranch, Turtle Cove, John Day river, Upper John Day beds, Oregon." **A,** Cranium in lateral view; **B,** maxilla with P3–M2 (white plaster fills voids in teeth); **C,** Eyerman's (1896) restoration of the holotype cranium and mandible. Note crushing and fragmentation of the cranium in (A).

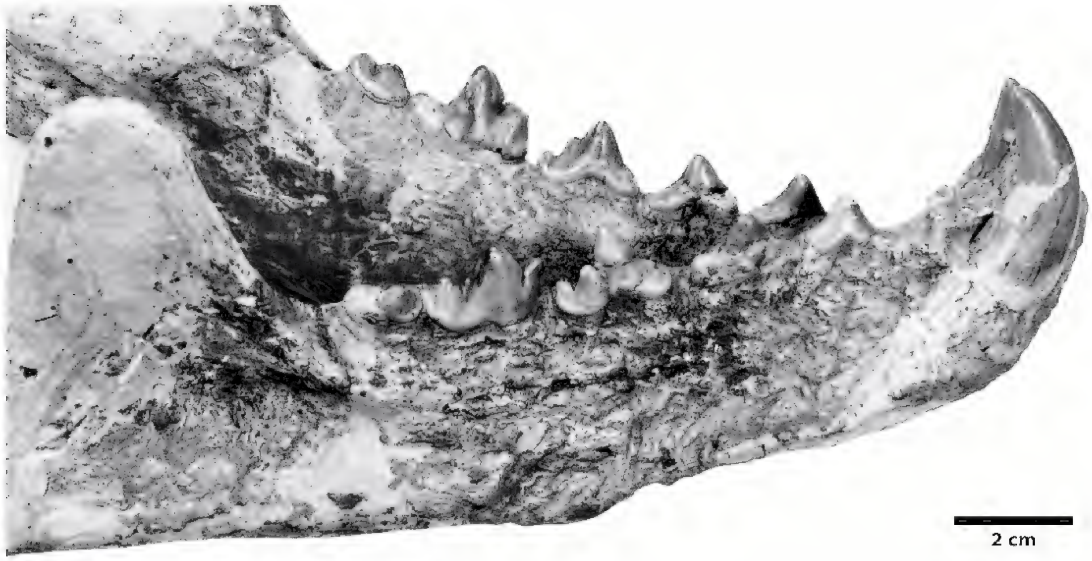


Fig. 13. Holotype mandibles of *Temnocyon ferox* Eyerman (YPM-PU 10787), with both canines and left and right p2–m2. Mandibular bone is heavily fractured. Associated forelimb, figure 53.

the tooth; the lingual cingulum was thickened, enlarging the protocone region, more so than in *T. subferox*. M1 retains both pre- and postprotocristae and the protocone is situated almost exactly in the center of the expanded lingual half of the tooth. M2 is much smaller than M1 and has markedly reduced the metacone; M3 is absent.

Relative to the wolf the upper and lower canines are larger whereas the incisors are the same size. Each lower incisor shows a single accessory cusp (Nebenzacke) on its labial margin.

A partially articulated postcranial skeleton, including the limbs, fore- and hind feet, was found in association with the skull and mandibles and was described by Eyerman (1896). Although difficult to free from the indurated matrix, the skeleton was prepared to demonstrate its limb proportions and digitigrade paraxonic fore- and hind feet. The limbs are discussed in the section on Postcranial Osteology.

DISCUSSION: *Temnocyon ferox* is distinguished from *T. altigenis* and *T. subferox* by larger size, similar to a living wolf, but shares with those species a plesiomorphic temnocyonine dentition. These three species probably form a morphocline in which body size increases through time. *T. ferox*, however, is the first species in this lineage to show specialization of its carnassials and molars, while still retaining simple low premolars that distinguish this species from *T. percussor*, *T. macrogenys*, and the species of *Mammacyon* and *Delotrochanter* that have larger more developed premolars. The presence of the m1 metaconid and short m2 are diagnostic features of the molars distinguishing *T. ferox* from temnocyonines of similar size such as *Mammacyon obtusidens* (which has no m1 metaconid and a larger, elongate m2) and *Temnocyon fingeruti*. *T. ferox* can be distinguished from *T. fingeruti* using M1–2: the *T. ferox* M1 shows a more developed lingual cingulum and M2 is much reduced whereas in *T. fingeruti* the M1 shows only modest expansion of the lingual cingulum and M2 is large. However, the M1 lingual cingula of both *T. ferox* and *T. fingeruti* are much less developed relative to the hypertrophied lingual cingula of *Mammacyon* and *Delotrochanter*.

Upper carnassials of *T. ferox* are damaged but appear to be sectorial teeth like those of *T. fingeruti*; however, P4 has a prominent protocone more lingually situated than in *T. subferox*.

The teeth of *Temnocyon ferox* are similar to the available teeth of *T. percussor* (p3–m2,

Fig. 14. Occlusal view of the holotype mandibles of *Temnocyon ferox* Eyerman (YPM-PU 10787), with left p2–4, m1–2, right p3–4, m1–2. An m1 metaconid is evident on both carnassials (stereopair).

M1). The size increase from *T. ferox* to *T. percussor* is characterized by development of a taller p3–4 and more robust m1–2 in *T. percussor*.

Temnocyon ferox is one of the few temnocyonines for which there is a confirmed association of the cranium and an articulated postcranial skeleton. Eyerman (1896) was aware of the evident disproportion between skull and limbs: the skull was larger than that of the average wolf yet the limbs were noticeably shorter. Limb elongation is nonetheless present, although not to the degree seen in the wolf. When compared with the limb and foot skeleton of the cursorial wolf, *T. ferox* shows a number of parallel adaptations (see Postcranial Osteology).

Forelimb elongation in *Temnocyon ferox* is evident relative to the plesiomorphic forelimb of *T. altigenis* and *Daphoenus*. As in the wolf, the forelimb of *T. ferox* exhibits a narrow distal humerus with reduced medial epicondyle, a closely apposed distal ulna and radius (i.e., articular process of the ulna reduced to a smooth planar facet pressed against the distal radius), and a digitigrade paraxonic forefoot with narrow carpus (metacarpals 2 and 5 short; metacarpal 1 reduced). In the hind foot there is a narrow elongated tarsus; long paraxonic metatarsals 3–4; shorter metatarsals 2 and 5; and metatarsal 1 a thin rodlike bone 45 mm in length (not as reduced as the minute triangular nubbin, 1 cm in length, that is the vestige of the first metatarsal of the wolf). Paraxonic metapodials of the fore- and hind foot of the wolf are ~2 to 2.5 cm longer than those of *T. ferox*. The lengthened radius and ulna and the long paraxonic metacarpals are responsible for the more elongate forelimb of the wolf.

Temnocyon percussor Cook, 1909
Figure 15

Temnocyon percussor Cook, 1909: 266, 271, fig. 3.

TYPE: AMNH 81005, associated right and left partial mandibles, left p3–m2, right p1, p4, m2, roots or alveoli of p2–3, m1, and a partial m3 alveolus, a doubtfully associated right upper canine, comprising Cook's (1909) type of *Temnocyon percussor*, found "about one-half mile west of Agate, Nebraska, in the Lower Harrison beds ....", Sioux County, Nebraska (see Discussion for additional information on site of collection). Cook's figure of the type is a composite based on both mandibles, although this is not plainly stated in his publication.

DISTRIBUTION: Late Arikareean, upper Arikaree Group, Sioux County, Nebraska.

DIAGNOSIS: Differs from *T. altigenis* and *T. subferox* in larger size and from *T. macrogenys* in much smaller size. Distinguished from *T. ferox* by taller differently proportioned p3–4 and by dimensions of m1–2 and M1 that together exceed the size attributable to a *T. ferox* population (tables 2, 3). *T. percussor* differs from *T. fingeruti* in having a taller more robust, somewhat longer p3–4, shorter m1–2, and no m2 metaconid. M1 lingual cingulum better developed in *T. percussor* relative to *T. fingeruti*.

REFERRED SPECIMENS: (1) AMNH 81054, right m1, American Museum–Cook Quarry (Hunt, 1972), 2 mi north of the Agate Spring Quarries, basal Anderson Ranch Fm., Sioux County, Nebraska, H. Cook, August 1909; (2) AMNH 81047, right M1, American Museum–Cook Quarry, basal Anderson Ranch Fm., Sioux County, Nebraska, H. Cook, July 1908.

DESCRIPTION: AMNH 81005—Cook (1909: 266) only briefly described this individual but presented an accurate illustration of the dentition. This illustration posterior to p3 is based on the left mandibular fragment, and anterior to p3 on the anterior part of the right mandible. It is not possible to estimate jaw depth since the lower border of the mandible has been broken away along the length of the horizontal ramus. However, an estimate of mandibular length, based on length of toothrow (c–m2, 110.9 mm), compares with the mandibular length of Eyerman's type of *T. ferox* (c–m2, ~102 mm), an observation complemented by the similar premolar spacing in both animals.

The p1 measures 8.4 mm in length, 5.0 mm in width. It is a small, single-rooted peglike tooth situated on the jaw margin anterointernal to the anterior root of p2. The main cusp is anteriorly inclined, and there are no accessory cusps.

The p2 is not preserved in either mandible; the alveolar measurements of length and width are 14.8 and 7.2 mm. The anterior root is more labially placed than the posterior root, the tooth being directed outward, a trait also seen in several other temnocyonines.

The p3 measures 15.9 mm in length, 7.8 mm in width. There are no posterior accessory or basal cingulum cusps. The tooth in lateral view is nearly an equilateral triangle, the posterior slope being only slightly longer than the anterior slope. Weak enamel ridges run down the anterior and posterior slopes; there is slight development of a lingual and posterior cingulum that is even less well defined labially.

The p4 measures 19.7 mm in length, 9.0 mm in width. It has the same form as p3, only larger and taller, with the addition of a prominent posterior accessory cusp and a shelflike heel at the rear of the tooth. The posterior accessory cusp is situated about half the distance down the posterior slope and is labial in position. A weak cingulum is present on the lingual and posterolabial faces of p4. A small cingular cusp also occurs on the shelflike heel of p4 where the posterior enamel ridge descends to meet it.

The m1 measures 23.5 mm in length, 10.5 mm in width. Trigonid length, 16.2 mm; talonid length, 7.3 mm. The trigonid appears somewhat inflated: paraconid and metaconid are of about equal height, the taller protoconid elevated only ~1.5 mm above the main p4 cusp. The metaconid is present, reduced, and situated on the posterolingual corner of the massive protoconid about half the distance to its base. The hypoconid is the only talonid cusp: it is centrally positioned, and occupies nearly all the talonid. A cingulum is developed on labial and lingual margins of the talonid. On the posterior slope of the hypoconid there

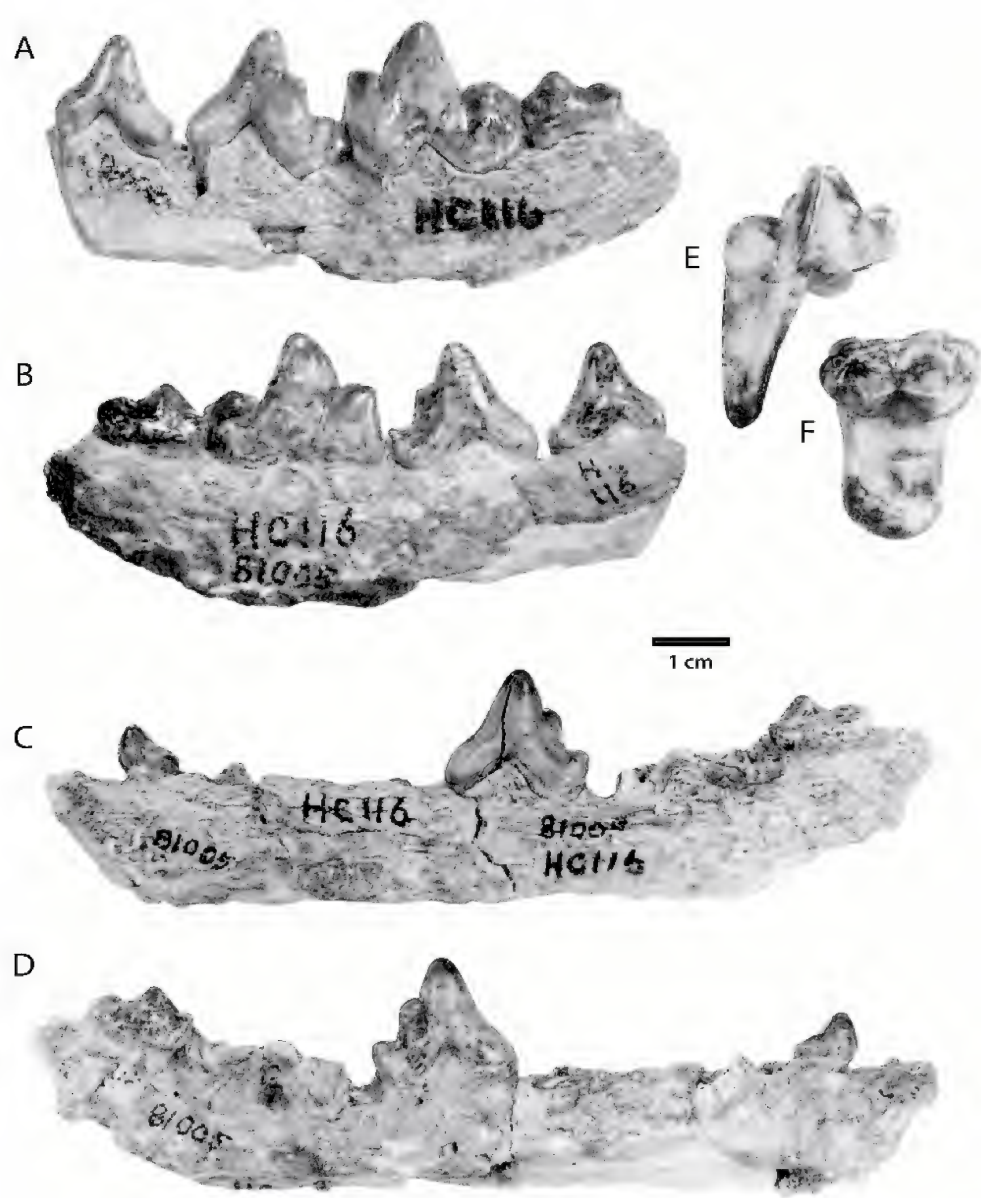


Fig. 15. *Temnocyon percussor* Cook, Niobrara River valley, Sioux Co., Nebraska. Holotype (AMNH 81005) left partial mandible with p3–m2 (**A, B**) and right mandibular fragment with p1, p4, and m2 (**C, D**) from 0.5 mi west of Agate Ranch headquarters, Harrison Formation, Sioux Co., Nebraska. **A, D,** labial and **B, C,** lingual views. Referred right m1 (**E,** AMNH 81054) and right M1 (**F,** AMNH 81047) from AMNH–Cook Quarry, basal Anderson Ranch Formation. Cook's 1909 drawing of the holotype is a composite of the two mandibular fragments (A to D) illustrated here, both from the same individual.

is a tiny cusp apparently derived from the cingulum.

The m2 measures 13.9 mm in length, 9.0 mm in width. The form of the tooth is most like m2 in YPM-PU 10787 (*T. ferox*) and differs from the elongate m2 of *Mammacyon*. The prominent m2 protoconid is the same height as the m1 hypoconid. These two cusps, aligned in series with the much smaller hypoconid of m2, are low, blunt, crushing instruments. A low paraconid occupies the anterolingual corner of m2. A low ridge

descends the protoconid to the lingual margin of m2. The m2 talonid is occupied solely by the low hypoconid placed directly behind the much larger protoconid. There is no entoconid.

The isolated upper canine measures 12.5 mm in labiolingual width at the enamel base; anteroposterior length, 17.2 mm; height, 61.2 mm. The tooth is recurved and exhibits a flat wear surface, ~25 mm in length, 6 mm in width, on the anterointernal face near the tip. The tooth is badly cracked, probably from postmortem drying prior to burial.

AMNH 81054—This isolated right m1 compares well with Cook's type m1 (AMNH 81005) but exhibits more wear. Although a vertical shear facet is evident on the labial face of the protoconid-paraconid, the tips of the protoconid, paraconid, and hypoconid are blunted by apical wear, suggesting mastication of hard material. This tooth measures 24.2 mm in length, 10.8 mm in width. The m1 talonid of AMNH 81054 is nearly identical to that of the holotype m1, including the cingular swelling on the posterior slope of the hypoconid.

Because they retain the m1 metaconid, *T. percussor* carnassials are easily confused with those of *Daphoenodon superbus*, the amphicyonid that occurs with *T. percussor* in the American Museum–Cook Quarry. In *T. percussor,* however, the hypoconid fills almost the entire talonid, but in *Daphoenodon* the hypoconid occupies only the labial talonid surface, and does not encroach on a narrow lingual talonid shelf. Isolated teeth in the American Museum–Cook Quarry demonstrate the presence of three beardogs (*Temnocyon percussor*, *Daphoenodon superbus, Ysengrinia americana*) at the site.

AMNH 81047—This isolated M1 was also found in the American Museum–Cook Quarry. Although not associated with other material of *T. percussor*, it has the form and predicted cusp morphology that correspond to mandibular teeth of the holotype. The tooth is an enlarged version of the M1 of *T. altigenis* and *T. ferox*, measuring 20.9 mm in length, 27.9 mm in width; hence it lacks the extremely swollen lingual cingulum found in *Mammacyon* and *Delotrochanter*. The paracone and metacone are conspicuously elevated above the lingual half of the tooth, forming a vertical shear surface. The paracone is somewhat larger than the metacone; both cusps are bordered by a sharply defined labial cingulum continuous with a prominent parastyle. The protocone is centrally situated on a flat enamel platform, and is less knob-like, more crescentic in form than in *Mammacyon*. A long preprotocrista runs from the protocone to the anterior cingulum, and a short low postprotocrista extends from protocone to posterior cingulum, similar in this respect to M1 of *T. ferox*.

The plesiomorphic form of the *T. percussor* M1 (AMNH 81047) is unique in the late Arikareean; the older *Mammacyon* lineage and contemporary *Delotrochanter* have more derived upper molars in which the protocone region forming the lingual half of M1 is more expanded, primarily due to the more swollen lingual cingulum. In AMNH 81047 the anteroposterior length of the protocone region is quite narrow relative to the length of the labial margin of the tooth (table 5), and its anterior cingulum is plesiomorphic (as in *T. altigenis*) in contrast to the enlarged cingulum of *Mammacyon*. The narrow M1 protocone region and the lack of a swollen anterior cingulum indicate the presence of a metaconid on the mandibular carnassial, and so AMNH 81047 cannot be referred to *Mammacyon* or *Delotrochanter* in which the m1 lacks a metaconid.

DISCUSSION: *Temnocyon percussor* is restricted to upper Arikaree Group sediments in western Nebraska, and has never been found outside of the Niobrara River valley near Agate in Sioux County. The species is more advanced in dental traits than the John Day holotype of *T. ferox*: *T. percussor* has broader, more robust teeth, taller premolars (p3–4), and a much larger yet still plesiomorphic M1. Although the two species are similar in dental features, the Great Plains *T. percussor* has a slightly longer m2 than found in the John Day *T. ferox* (ratio E/F is ~1.7 in AMNH 81005, ~1.8 in YPM-PU 10787, table 6). Eyerman's type (YPM-PU 10787) of *T. ferox* represents a smaller individual than *T. percussor* and a less evolved dental stage, suggesting an older age for the John Day carnivore.

Cook (1909) was aware that the holotype, found by him in 1906, was dentally similar to

the John Day *T. ferox* yet represented a larger carnivore with different p3–4 proportions. The M1 later found by Cook in 1908 is reasonably referred to *T. percussor*, its large size and form in agreement with the m1–2 of the holotype mandible.

If Cook (1909) correctly attributed the holotype of *Temnocyon percussor* (AMNH 81005) to the *Syndyoceras* level or "quarry" one-half mile west of Agate, then the holotype material comes from the Harrison Formation about 40–50 ft (12–15 m) below the upper contact of the formation with the Anderson Ranch beds. The isolated molars (AMNH 81054, 81047) come from the American Museum–Cook Quarry in the basal Anderson Ranch Fm., about 50 ft stratigraphically higher than Cook's AMNH 81005. The *Syndyoceras* level is late Arikareean in age and occurs in proximity to the Agate Ash, initially 21.3 Ma (KA 481, Evernden et al., 1964), now more recently dated by the $^{40}Ar/^{39}Ar$ method at ~22.9 Ma (Izett and Obradovich, 2001). The similarity of the teeth of *T. percussor* and *T. ferox* suggests a relationship: although the age of *T. ferox* is uncertain (see Age and Correlation), a date older than 22.9 Ma is supported by its less advanced dentition relative to the more robust teeth of T. *percussor*.

The presence of *T. percussor* (with m1 metaconid) in western Nebraska in both the Harrison Formation and basal Anderson Ranch beds in the Agate area, and the occurrence of large *Delotrochanter oryktes* (without m1 metaconid) in these same two formations, also in the Agate area, demonstrates that the temnocyonine dentition was evolving at different rates in these two contemporary lineages. This had been difficult to prove given the fact that two or more temnocyonine species rarely occur in proximity in the same rock unit. However, based on fossils in this study, two temnocyonine genera had already lost the m1 metaconid prior to the late Arikareean (*Mammacyon*, LACM 9194; *Delotrochanter*, CM 1603); hence these represent more derived dentitions relative to a geologically younger *Temnocyon percussor* that retains its m1 metaconid and plesiomorphic M1 into the late Arikareean interval. If *T. percussor* directly precedes *T. macrogenys*, which is probable, then *Temnocyon* maintains this plesiomorphic dental pattern in the Great Plains until its extinction at the end of the Arikareean.

Temnocyon fingeruti, new species
Figures 16–19, 68

TYPE: NM 280/61, a complete skull and lower jaws in articulation, the rostrum offset ~3 cm from the posterior cranium by sediment deformation after burial; both left and right I1–3, C, P1–4, M1–2 and left i3, c, p2–4, m1–3, right c, p1–4, m1–3, from the Haystack Valley Member (revised), John Day Formation, Oregon, Lower Beardog Section, E1/2, NE4, SW4, SW4, sec. 27, T8S, R25E, Kimberly 7.5-minute quadrangle, from 96 ft stratigraphic level in appendix 1–6, Hunt and Stepleton (2004: 81); 62 ft above a radioisotopically dated horizon at ~23.8 Ma.

DISTRIBUTION: Latest Oligocene, late mid-Arikareean, John Day Formation, Wheeler County, Oregon.

ETYMOLOGY: The species name recognizes Michael Fingerut, who discovered and collected the holotype in the Balm Creek drainage, north-central Oregon.

DIAGNOSIS: Wolf-sized species of *Temnocyon* (basilar skull length ~25 cm), distinguished from *T. altigenis* and *T. subferox* by much larger size, from *T. macrogenys* by smaller size; differs from similarly sized *T. ferox* by greater inflation of the frontal paranasal sinuses (relative to braincase width, table 7) and by different form and proportions of p4–m2 and M1–2 (tables 2, 3), including a more lingually extended M1–2 with less expansion of M1 protocone region (ratio A/B, table 6), a much larger M2 and m2, a longer m2 (ratio E/F), and by a more robust, wider p4. *Temnocyon fingeruti* differs from *T. percussor* in its much smaller M1 (in the upper dentition of *T. percussor* only M1 survives), more elongate m1–2, stronger m1 metaconid, and larger, rectangular m2 with vestigial metaconid and more developed paraconid, and by the p4/m1 ratio (0.78 in *T. fingeruti* vs. 0.84 in both *T. percussor* and *T. ferox*). *Temnocyon fingeruti* differs from *T. altigenis*, *T. subferox*, and probably *T. ferox* in P4 proportions (ratio C/D, table 6); P4 is not known in *T. percussor* and *T. macrogenys*.

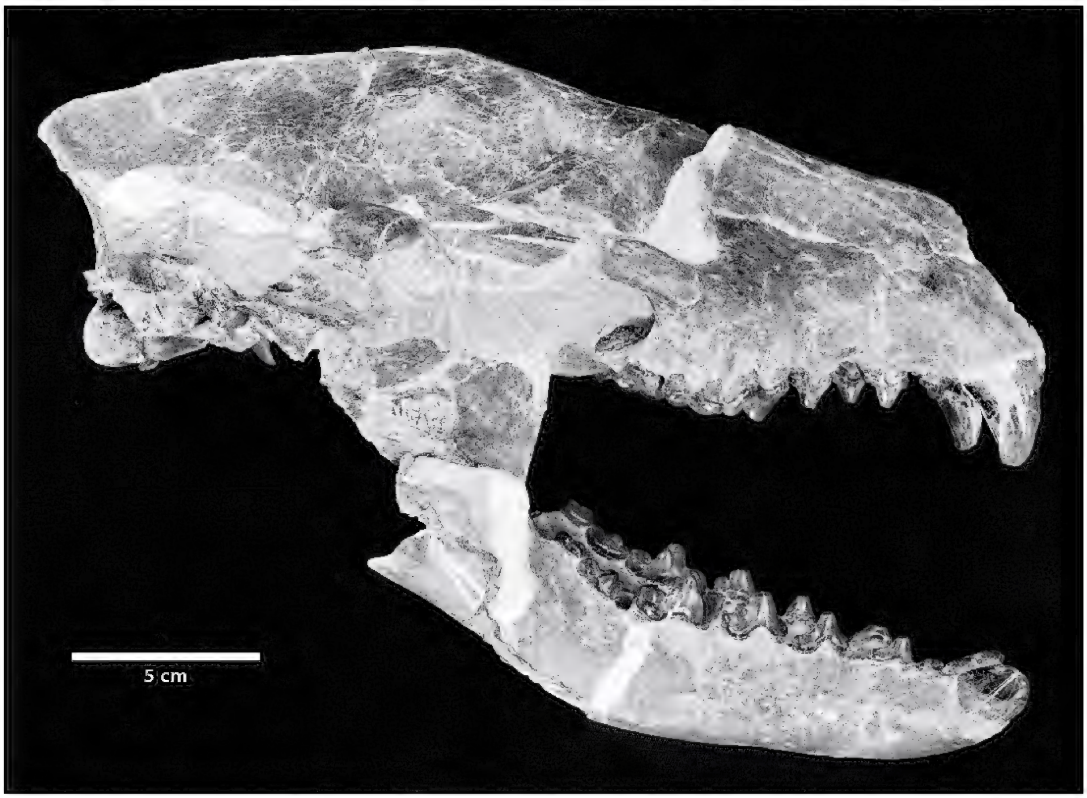


Fig. 16. Holotype cranium and mandibles of *Temnocyon fingeruti* (NM 280/61), from Balm Creek, Haystack Valley Member (revised), John Day Formation, Wheeler Co., Oregon. This skull was found 62 ft (~19 m) above a tuffaceous horizon dated to ~23.8 Ma (Hunt and Stepleton, 2004).

REFERRED SPECIMENS: None.

DESCRIPTION: The skull of NM 280/61 is elongate (basilar length, 25 cm, table 7) as are the known skulls of *T. ferox* and *T. subferox* but differs from the short, broad skull of *Delotrochanter oryktes*. Cranial size and proportions are similar to those of *T. ferox* except for the much greater frontal sinus inflation and entirely different form of P4–M2 and p4–m2 in *T. fingeruti*. Despite smaller size, a narrower snout and clearly dissimilar dentition, the profile of NM 280/61 compares with the skull form of *Mammacyon ferocior*. NM 280/61 approximates a large male wolf (*Canis lupus*) in rostral proportions and palatal dimensions but shows a longer postorbital cranium with broader basicranium, greater frontal sinus inflation, and smaller braincase volume. Although the teeth are similar in occlusal dimensions to those of a wolf, NM 280/61 has larger canines, more robust premolars, with a proportionately smaller shearing m1 and a longer m2–3 crushing platform. As with other John Day crania, sutures and anatomical detail are obscured by diagenetic alteration of bone. The orbital region preserves the orbital foramina nested in the elongate depression previously descibed for *T. altigenis* (UCMP 1549). An orbital foramen, sphenorbital fissure, and anterior opening for the alisphenoid canal (the foramen rotundum opening internally into the canal) are situated as in that plesiomorphic species, and it is apparent that this anatomical pattern is common to all temnocyonines where the orbital region has been preserved. The basicranium and auditory region are exceptional and are discussed in the section on Basicranial Anatomy.

The mandible is gracile and slender (depth beneath m1, 32 mm; below p2, 27 mm) with toothrow length (p1–m3) of 110 mm. These teeth are worn, indicating a mature but not aged individual; the canines, particularly the

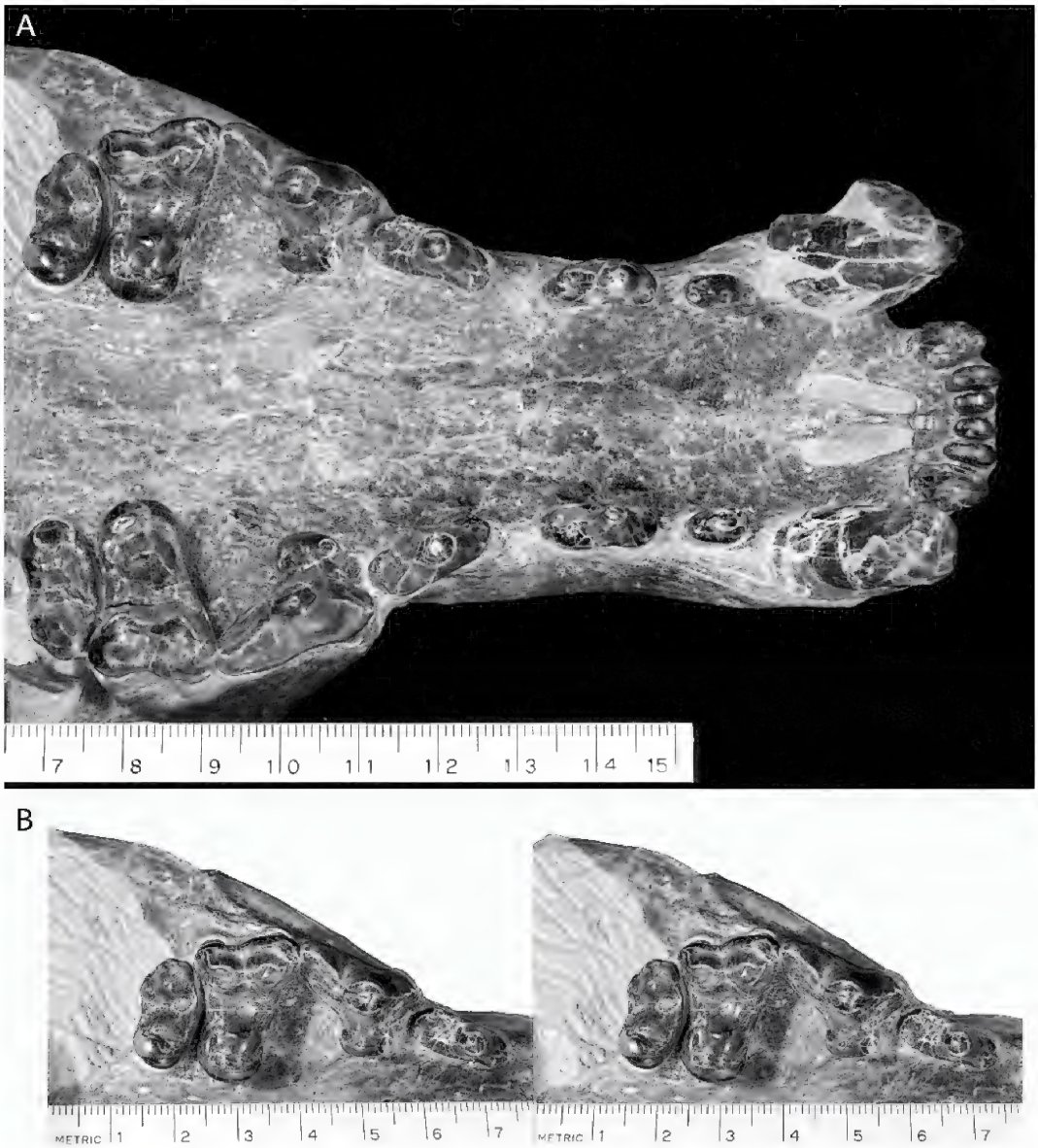


Fig. 17. Holotype palate and upper dentition (**A,** left and right I1–3, C, P1–M2; **B,** stereopair with right P3–M2) of *Temnocyon fingeruti* (NM 280/61), Balm Creek, Haystack Valley Member (revised), John Day Formation, Wheeler Co., Oregon. Note occlusal wear on P3–M2.

lower pair, reflect some damage, with the right lower canine beveled to a rounded stub suggesting it had been broken and smoothed by abrasion during life.

Lower incisors of temnocyonines rarely survive but are preserved in *T. fingeruti*. The i1–3 were quite small; there is little room (~1 cm) for them between the canines. During feeding these incisors would have been of little use. A somewhat larger i3 (length, 6.4 mm; width, 3.7 mm) contrasts with i2 (length, 5.9 mm; width, 2.9 mm) represented only by a broken root. There is no evidence of i1 that if present was placed in front of and *below* i2.

The canine measures ~19 mm in length, ~10 mm in width, measured at the enamel base; the symphyseal width is narrow, only

Fig. 18. Holotype left (**A**) and right (**B**) mandibles of *Temnocyon fingeruti* (NM 280/61), from Balm Creek, Haystack Valley Member (revised), John Day Formation, Wheeler Co., Oregon, both in labial view (left c, p2–m3; right c, p1–m3).

30 mm measured across the base of the canines.

The p1 is a small, peglike tooth (length, 6.9 mm; width, 4.0 mm) and is much worn.

The p2 (length, 12.1 mm; width, 5.6 mm) is much larger than p1 with its posterior slope somewhat longer than the anterior slope. A thin enamel ridge travels down both the anterior face to the anterolingual corner and the posterior face to the posterolabial cingulum. There are no accessory cusps.

The p3 (length, 15.3 mm; width, 6.6 mm) is a larger replica of p2 with a small posterior cingular shelf and a tiny basal cusp; the shelf is indented by wear on the left p3, less so on the right. There are no evident accessory cusps.

The p4 (length, 19.3 mm; width, 8.7 mm) is quite long relative to p3. There is a prominent labially situated posterior accessory cusp above a cingular shelf.

The principal cusps of p2–4 are worn flat by apical abrasion. The p2–3 are not tall relative to those in the large durophagous species of *Mammacyon* and *Delotrochanter*. They compare with p2–4 of *T. altigenis* but are much larger teeth.

The m1 (length, 24.7 mm; width, 10.6 mm) is a narrow, shearing carnassial that in this individual shows apical wear on trigonid and talonid cusps. Although the mandible of *T. fingeruti* and the wolf are of similar size, m1 is much smaller and the premolars larger in the beardog. The paraconid is mesially advanced to form a shear plane with the tall protoconid. A prominent metaconid is situated posterolingual to the protoconid. The talonid is filled by a large hypoconid; this cusp does not attain the height of the paraconid as in *Mammacyon* and *Delotrochanter*. A sinuous labial cingulum is present on the talonid but subdued on the trigonid. There is no entoconid yet a very narrow lingual talonid shelf occurs.

The elongate m2 (length, 14.8 mm; width, 8.9 mm) displays a low paraconid anterolingual to the taller, rather blunt, labial protoconid; a small metaconid is present.

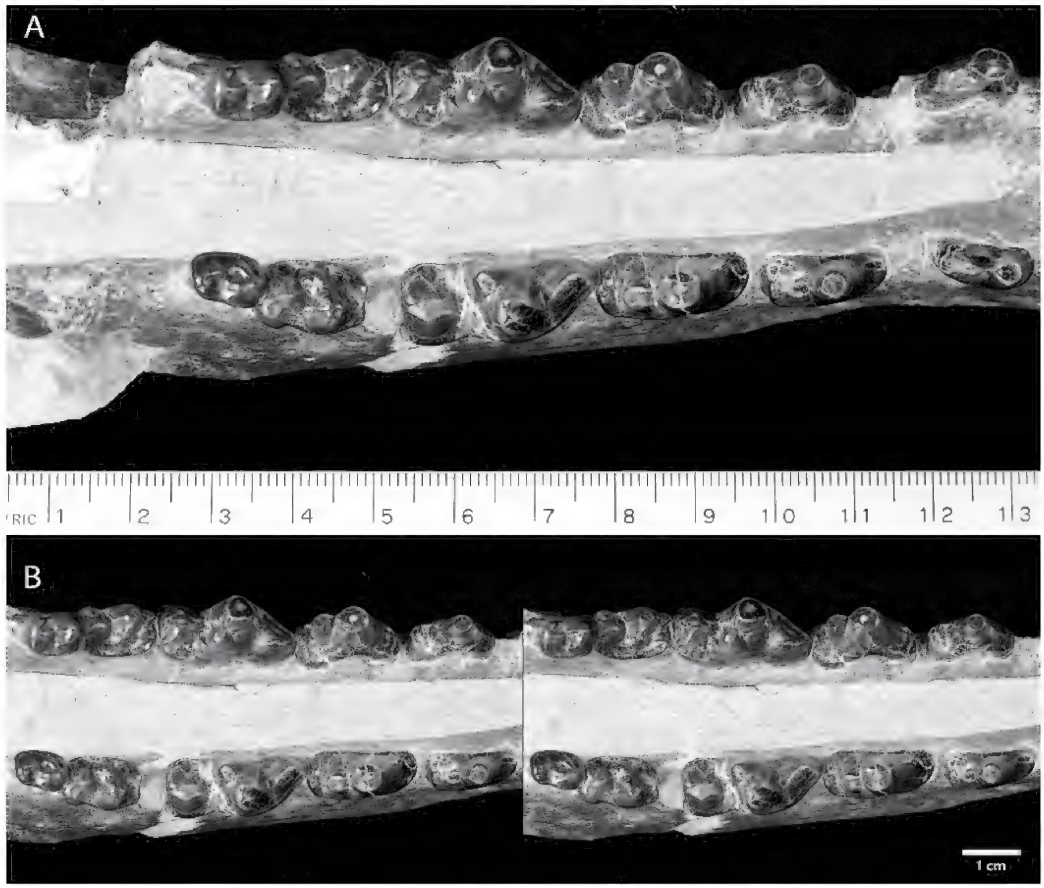


Fig. 19. Occlusal views of the mandibular dentition of the holotype of *Temnocyon fingeruti* (NM 280/61). Balm Creek, Haystack Valley Member (revised), John Day Formation, Wheeler Co., Oregon. **A,** left and right p2–m3; **B,** stereopair of p3–m3. Note apical wear on premolars and carnassials.

The m2 talonid has a low, more centrally placed hypoconid; there is no entoconid.

The rectangular m3 (length, 9.8 mm; width, 7.1 mm) has a distinct trigonid somewhat elevated above the talonid. The protoconid is connected by a curvilinear ridge to a very small metaconid. A low hypoconid is the only talonid cusp. A cingulum surrounds both the m2 and m3.

The upper dentition is one of the most complete among temnocyonines. Both toothrows are intact: width of the transverse incisor row, 24.7 mm; width between canines, 24.9 mm; a narrow palate between P1–2 (25.9 mm) widens between P3–4 (36.8 mm), and reaches its maximum breadth (59 mm) between the embrasures of the P4–M1 pair. Palatal length measured from I1 along the midline to the posterior border of the palate is 13 cm. Toothrow length from P1–M2 is 92.1 mm (P2–4, 58.7 mm; M1–2, 27.3 mm).

I1 (length, 5.5 mm; width, 2.4 mm) and I2 (length, 6.5 mm; width, 2.7 mm) are quite small, their apices worn flat. I3 is larger (length, 10.0 mm; width, 5.4 mm), heavily worn to a stub. There are short diastemata between I3 and the canine (4.8 mm), between C–P1 (3.6 mm), P1–2 (3.9 mm), P2–3 (7.0 mm), and P3–4 (2.0 mm). The small I3 of *T. fingeruti* contrasts in size with the huge I3s of *D. oryktes* and *M. ferocior*. Wear on the upper incisors of *T. fingeruti* shows that they occluded with i1–3 in a grasping or nipping role.

The canine (length, 17.3 mm; width, 12.3 mm, measured at enamel-dentine contact) is broken and worn, but it was more robust than a wolf canine from a similarly sized skull.

P1 is a small peglike tooth (length, 7.6 mm; width, 4.7 mm) with a low vertical anterior face and a posterior slope lacking accessory cusps.

P2 is a larger triangular tooth (length, 13.4 mm; width, 5.7 mm) with a posterior slope slightly longer than the anterior face. There are no accessory cusps.

P3 is somewhat larger (length, 16.1 mm; width, 7.0 mm) than P2 with anterior and posterior faces as in P2 but having a broader heel than P2. Heavy wear on the posterior slope prevents identification of an accessory cusp but it was probably not present.

P4 is a short carnassial (length, 22.0 mm; width, 15.4 mm) with a prominent shear plane beveling the lingual faces of paracone and metastylar blade. A blunt protocone is situated directly lingual to the paracone. The posterior half of the protocone occluded against the m1 paraconid, evidenced by an elliptical wear facet, whereas the anterior face of the protocone was abraded by the p4 accessory cusp. Labial and lingual cingula are present but the anterior face of P4 and the adjacent heel of P3 were deeply worn by the principal and accessory cusps of the large p4.

The principal cusps of P1–3 exhibit flat apical wear facets. This blunting of cusps also occurred on the M1 paracone and metacone (with minor apical wear on M2 paracone) and the paracone and metastylar blade of P4. P4 wear included a shear component that extended posteriorly along the lingual faces of the M1 paracone-metacone and M2 paracone, evidenced by shear facets on these molars.

M1 (length, 17.1 mm; width, 22.4 mm) retains a plesiomorphic occlusal form little different from that of *T. altigenis*. The paracone and slightly smaller metacone are bordered by a labial cingulum with developed parastyle. The cingulum thins on the margins of M1 at the level of the protocone basin but then thickens to form a prominent posterolingual cingulum around the protocone, which does not equal the strongly swollen M1 lingual cingula observed for *Mammacyon* and *Delotrochanter*. The protocone is situated near the anterior margin of the tooth and is more sharp-crested and less bunodont. A preprotocrista runs anterolabially from the protocone to the anterior cingulum, and a short weak postprotocrista intersects the posterior cingulum.

M2 (length, 9.6 mm; width, 17.4 mm) is smaller and of a different form than M1; the anterior margin is convex, the posterior concave. The paracone is much larger than the low reduced metacone yet the lingual face of the two cusps forms a vertical shear plane. The labial and anterior sides of M2 are bordered by a cingulum that thickens to form a wide lingual swelling. A minute protocone situated in the center of an enamel flat retains an anterolabially directed preprotocrista and a tiny postprotocrista. The posterior margin of M2 is worn by the anterior face of m3 since there is no M3.

In *T. fingeruti*, crushing/shearing occlusion was accomplished by p4–m2 and P3–M2. More anterior teeth served to grasp the food and, via the action of the tongue, passed it back to the carnassials and molars.

Discussion: The skull and mandibles of NM 280/61 represent one of the best-preserved North American temnocyonines. The species preserves the most wolflike dentition of any temnocyonine and exhibits an attritional dental wear pattern much like that known for *Canis lupus*. Despite some crushing of the skull that collapsed the zygomata and shifted the rostrum laterally relative to the frontal region, the cranium, teeth, and basicranial anatomy are exceptional. NM 280/61 demonstrates that a plesiomorphic temnocyonine dental pattern continued in the Pacific Northwest to very near the Oligocene-Miocene boundary, currently placed at 23.03 Ma (Gradstein et al., 2004). Because NM 280/61 occurs only ~20 m above a radiometric date of 23.8 Ma, its stratigraphic level places it in the latest Oligocene.

NM 280/61 is the stratigraphically youngest John Day temnocyonine yet discovered; whether Great Plains early Miocene temnocyonines such as *T. macrogenys* and *Delotrochanter* existed in the Pacific Northwest is not known. Absence of early Miocene temnocyonines in the John Day beds could simply reflect the more limited representation of sediments of that age, which are often unfossilferous. However, large daphoenine and amphicyonine beardogs have been found in early Miocene John Day strata of early Hemingfordian age (*Borocyon*, *Amphicyon*:

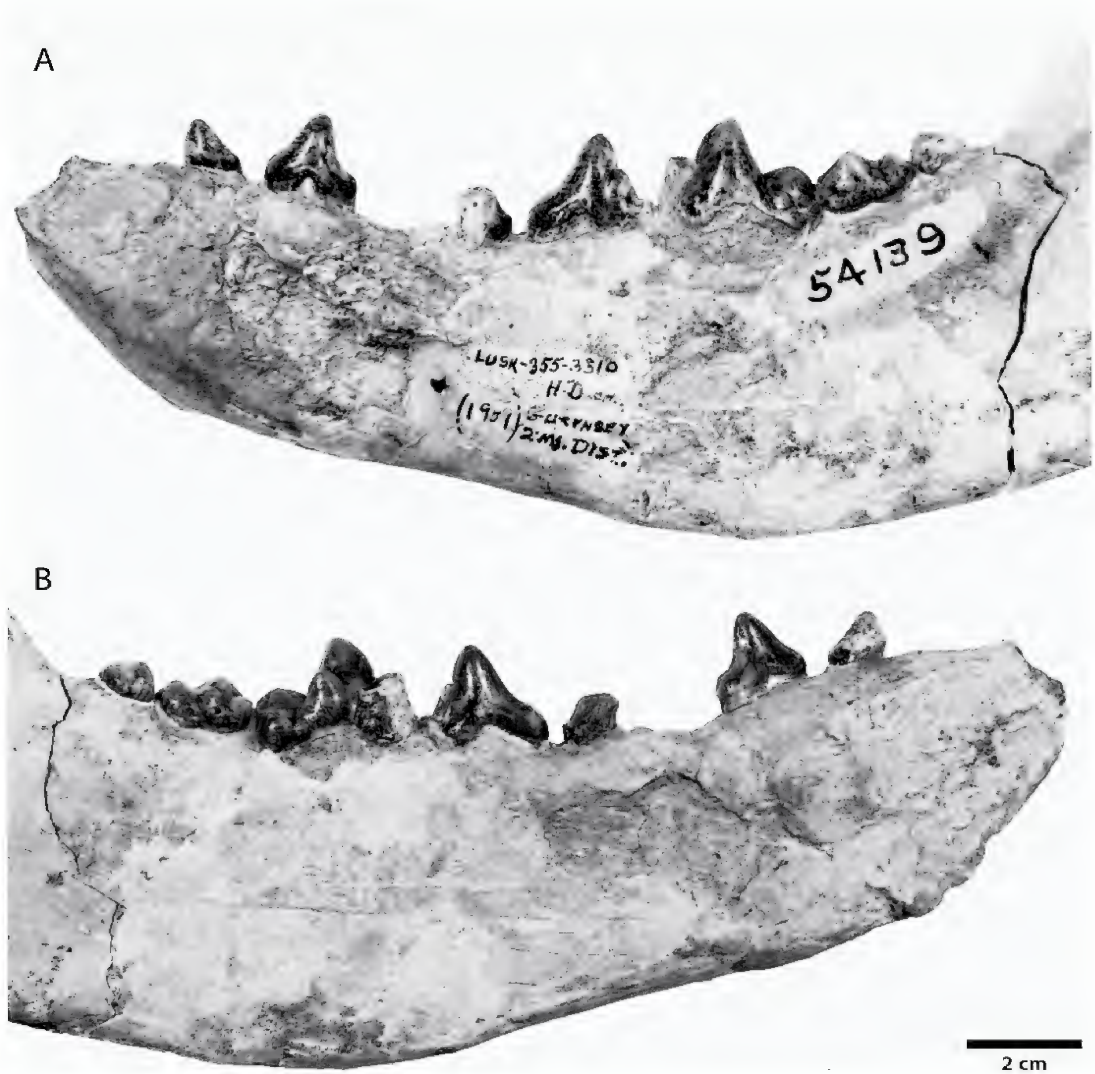


Fig. 20. Holotype mandible of *Temnocyon macrogenys* (F:AM 54139), with left p1–2, p4–m3 (pathologic p3), Anderson Ranch Formation, 2-Mile District, near Guernsey, Platte Co., Wyoming. This is the largest and youngest species of *Temnocyon*. **A,** labial and **B,** lingual views.

Hunt and Stepleton, 2004), suggesting that they replaced the temnocyonines.

Temnocyon macrogenys, new species
Figures 20, 21

TYPE: F:AM 54139, left mandible with canine alveolus, p1–2, broken roots of pathologic p3, complete p4–m3, with most of the ascending ramus, articular condyle, and angular process preserved; also two partial metapodials and a fragmentary astragalus, from the Anderson Ranch Fm., "High Daemonelix zone," 2-Mile District of Charles Falkenbach, near Guernsey, Platte County, Wyoming, collected by C. Falkenbach, 1939.

DISTRIBUTION: Latest Arikareean, Anderson Ranch Fm., Platte County, Wyoming.

ETYMOLOGY: From the Greek, *macro*, "long," and *genys*, "jaw," in reference to the large, elongate mandible of the terminal species of the *Temnocyon* lineage.

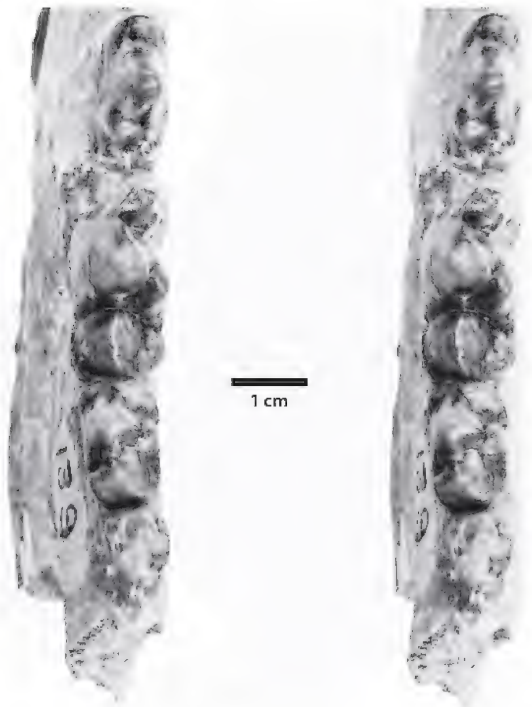


Fig. 21. Occlusal steropair of the holotype dentition (p4–m3) of *Temnocyon macrogenys* (F:AM 54139). Note presence of m1 and m2 metaconids.

DIAGNOSIS: Largest species of *Temnocyon* (basilar length, ~30 cm, table 7), and the only large temnocyonine in which the plesiomorphic cusp pattern of the lower teeth is retained: m1 shear maintained; metaconids present on m1–2; m1/m2 ratio, 1.62, the lowest among *Temnocyon* species (table 6). Depth of mandible below m1, ~50 mm; below p2, 46 mm. Mandibular dental measurements highest values among species of *Temnocyon*: length of toothrow, p1–m3, 135 mm; lengths in mm of p2, 16.6; p4, 22.1; m1, 28.2; m2, 17.4 (table 2).

REFERRED SPECIMENS: None.

DESCRIPTION: The nearly complete mandible lacks only part of the ventral border of the horizontal ramus and small sections from the labial and lingual sides. From the anterior limit of the jaw to the posterior face of the articular condyle is ~26 cm; this is a large carnivore with estimated basilar skull length of 30 cm, thus the largest known temnocyonine. The articular condyle and angular process are in close proximity: from the center of the condyle to the process is 24 mm. The distance from the tip of the coronoid process to the articular condyle is 77 mm; from tip of coronoid to base of angular process is 106 mm. The coronoid process is gently recurved posteriorly, with a shallow depression on its lingual face, and a moderately deep masseteric fossa on the buccal face. The articular condyle, mandibular foramen, and coronoid and angular processes are configured as in *Canis lupus*. Except for the much greater size and mandibular depth of the beardog, the form of the jaw is similar to that of the wolf. As in other temnocyonines, the anterior border of the ascending ramus is gently inclined so that m2–3 are slightly elevated and tilted forward on the edge of the ramus. Depth of the mandible below p2 is 46 mm, beneath m1 ~50 mm, thus differing from *Delotrochanter oryktes* (ACM 4804) for which the same measurements, respectively, are 46 and 42 mm, and for *Mammacyon obtusidens* (LACM 9194), 38 and 35 mm. The mandibular depth beneath m1 for *T. macrogenys* is nearly twice that of an average wolf.

The mandibular symphysis was united by strong binding ligaments; there is no evidence of symphyseal fusion. The symphysis is widest near its posterior edge. The greatest anteroposterior length is ~56 mm; greatest dorsoventral height ~37 mm. The upper part of the symphysis (a rectangular area 22 mm in length, 11 mm in width) is smoother and less rugose than the ventral portion and represents the attachment of a compressible fibrocartilage pad like that described by Scapino (1981; Hunt, 2009). This indicates a flexible mandibular symphysis in *T. macrogenys* that facilitates close registration of the carnassials during the bite, as in the wolf (fig. 50F).

None of the lower incisors are preserved, however the extremely narrow space between the symphysis and canine alveolus shows that they would have been very small teeth.

The large canine alveolus measures 26.5 mm in length, 20.7 mm in width, with the long axis of the ellipse directed anteriorly and somewhat laterally. There is no intervening space between the canine and p1, their alveolar borders nearly in contact.

Premolars (p2–4) are not crowded and are separated by 2–3 mm diastemata; they are not shortened or posteriorly widened as in *Delotrochanter* but are relatively narrow, tall yet robust, thus representing a scaled-up version of the premolars of *T. percussor*.

The single-rooted p1 measures 10.6 mm in length, 7.3 mm in width. It has the form of an oblate cone, anteriorly inclined, whose posterior face has been slightly depressed. There are no accessory or basal cusps. A fine enamel ridge runs from the principal cusp down the posterior slope to the cingulum.

The p2 measures 16.6 mm in length, 8.5 mm in width. In lateral view it approximates an equilateral triangle; there are thin anterior and posterior enamel ridges but no posterior accessory cusp. There is a moderately developed heel with a very small, low basal cusp.

The p3 is represented only by the posterior basal part of the tooth. The tooth was either abnormally triple-rooted, or there was a supernumerary single-rooted premolar inserted in front of a normal p3, this latter alternative more probable. The three alveoli occur in anteroposterior sequence, with a total alveolar length of 24.9 mm. This is longer than p4. If a normal p3 was present, its length based on alveoli would be ~18 mm.

The p4 measures 22.1 mm in length, 10.4 mm in posterior width, 8.5 mm in anterior width. There is a prominent, labially placed posterior accessory cusp. The posterior border of the tooth is squared and produced as a shelf with a small basal cusp situated below the posterior accessory cusp. Height of p4 is much greater than the m1 paraconid, and I suspect that were p3 present, it also would exceed the paraconid in height.

Length of the premolar series (p1–4) is ~82 mm. However, because this measurement includes an abnormality (p3), it probably represents a maximum value for the species.

The m1 measures 28.2 mm in length and a talonid width of 13 mm. Length of the trigonid is ~20 mm, the talonid ~9.5 mm, emphasizing that the trigonid dominates the tooth and the talonid is not enlarged. The metaconid is well developed; this is the only large temnocyonine in which the metaconid survives. The short talonid is dominated by a large, labially situated hypoconid, directly behind the protoconid. The labial face of the asymmetric hypoconid descends abruptly to the cingulum but the lingual face is more gradually inclined, sloping to the medial edge of the talonid (there is a small lingual talonid shelf). The apex of the hypoconid is an anteroposteriorly aligned ridge that curves posterolingually to become the posterior edge of the talonid. There is weak swelling on the lingual talonid shelf that appears to be a vestigial entoconid.

The m2 measures 17.4 mm in length, with a talonid width of 10.0 mm, and a trigonid width of 10.4 mm. The trigonid is low but higher than the talonid. There is an anterolabial cingulum; the large protoconid is the most prominent cusp and is connected by a smoothly curving ridge to the low, broad paraconid. The small knoblike metaconid lies lingual to the protoconid and is separated from it by a slight constriction. The hypoconid is the only talonid cusp and is labial in position. The talonid surface descends gradually from the hypoconid to the lingual margin.

The m3 measures 10.7 mm in length, ~8.5 mm in width. The only prominent cusp is a conical protoconid, somewhat anterior to the center of the tooth, flanked lingually by weak enamel ridges descending to barely discernible vestigial paraconid and metaconid swellings. The talonid is much reduced and shows only a vestige of the hypoconid as a swelling on the posterior face of the protoconid.

The toothrow measures as follows: anterior border of canine alveolus to m3, 160.9 mm; p1–m3 length, 135.0 mm; p1–m2 length, 125.4 mm; m1–3 length, 55.5 mm.

DISCUSSION: *Temnocyon macrogenys* is the largest North American species of the genus and it retains the metaconid on m1–2. The m1 remains a shearing carnassial (i.e., a tall, shearing trigonid and low talonid), and the premolars, although robust, are tall, relatively narrow teeth. These dental features indicate a large predatory carnivore with a more sectorial dentition than found in *Mammacyon* and *Delotrochanter*. When compared to the mandibular dentition of the wolf, the canine, premolars, and m2–3 of *T. macrogenys* are much larger whereas the carnassial

is the same length, although a broader tooth. The beardog has incorporated the carnassial as an integral part of a crushing dental battery made up of premolars and posterior molars, while still retaining some shearing ability.

The dentition of *T. macrogenys* can be derived from that of *T. percussor*, and there is a particularly strong similarity in cusp pattern to AMNH 81005, Cook's type of the species. This opinion is supported by m1–2 structure and similar m1/m2 length ratios of 1.62 and 1.69 in AMNH 81005 and F:AM 54139 (table 6). *Temnocyon macrogenys* seems the lineal descendant of *T. percussor* from the Niobrara River valley at Agate National Monument.

Temnocyon macrogenys (F:AM 54139) comes from the Anderson Ranch beds about 2 mi south of Guernsey, Wyoming; in this district and throughout northwest Nebraska and southeast Wyoming the formation includes widespread flat geomorphic surfaces representing level, early Miocene grasslands (Hunt, 1990). These surfaces are densely packed with fine root casts (rhizoliths) and are cemented by silica derived from diagenesis of volcanic glass shards and unstable minerals in these fine-grained tuffaceous sandstones. Charles Falkenbach, who collected the mandible of *T. macrogenys*, used the term "High Daemonelix zone" for these silica-cemented geomorphic surfaces, although they have no relationship to rodent burrows first termed "Daimonelix" many years previously by E.H. Barbour (1892). Evidence that Falkenbach in fact collected the mandible from one of the geomorphic surfaces of the Anderson Ranch Formation can be seen in the sediment adhering to the mandible that includes the small siliceous rootlets and pale reddish-brown sand typical of these grassland surfaces. *Temnocyon macrogenys* was found within one of these siliceous paleosols. Fossil mammals in the Childs Frick collection from the "High Daemonelix" level of the Guernsey collecting district are similar to mammals of the Niobrara Canyon local fauna from the stratotype area of the Anderson Ranch Formation (Niobrara Canyon, Sioux County, Nebraska) and establish the age of *T. macrogenys* as latest Arikareean.

Rudiocyon, new genus

TYPE SPECIES: *Rudiocyon amplidens*, new species.

INCLUDED SPECIES: Only the type species.

DISTRIBUTION: Early or mid-Arikareean of Oregon.

ETYMOLOGY: From the latinized Greek, *kyon*, for "dog," and for Rudio Creek, the locality in north-central Oregon where the holotype was discovered.

DIAGNOSIS: Differs from *Temnocyon* by absence of the m1 metaconid; from *Mammacyon* and *Delotrochanter* by a small, short m2 relative to m1 (table 6, ratio E/F ~1.9); and from *Delotrochanter* by a narrow, compressed p4 (not posteriorly broad). See tables 1–2.

DISCUSSION: The genus includes a single species represented by a partial mandible with massive teeth (p4–m2) that define the taxon. A small m2 in *Rudiocyon* (table 6, ratio E/F, ~1.9) precludes assignment to *Mammacyon* (table 6, ratio E/F, 1.57–1.6), a genus defined by a large, elongate m2. Nonetheless, the genus may have evolved from an earlier less derived species that gave rise to both *Mammacyon* and *Rudiocyon*. Similarity to cheek teeth of *T. ferox* suggests a possible alternative derivation for *R. amplidens*. *Rudiocyon amplidens* is considered somewhat younger than the age of the Deep Creek tuff (27.9 ± 0.57 Ma); the probable site of collection occurs 10–15 m above a local ash on Rudio Creek identified as a correlative of the Deep Creek tuff.

Rudiocyon amplidens, new species
Figures 22, 23

Temnocyon large species: Stock, 1933b: 36.

TYPE: LACM 480, partial left mandible with p4–m2, right m2, right p4 protocone, and a partial braincase, from the John Day Formation, CIT loc. 31, 1.5 to 2 mi south of the Johnson Ranch [now Tom Campbell Ranch] at the mouth of Rudio Creek, from gray beds exposed on the east side of Rudio Creek, south of the North Fork of the John Day River, Grant County, Oregon, collected by E.L. Furlong (~1930).

DISTRIBUTION: Early or mid-Arikareean, John Day Formation, Grant County, Oregon.

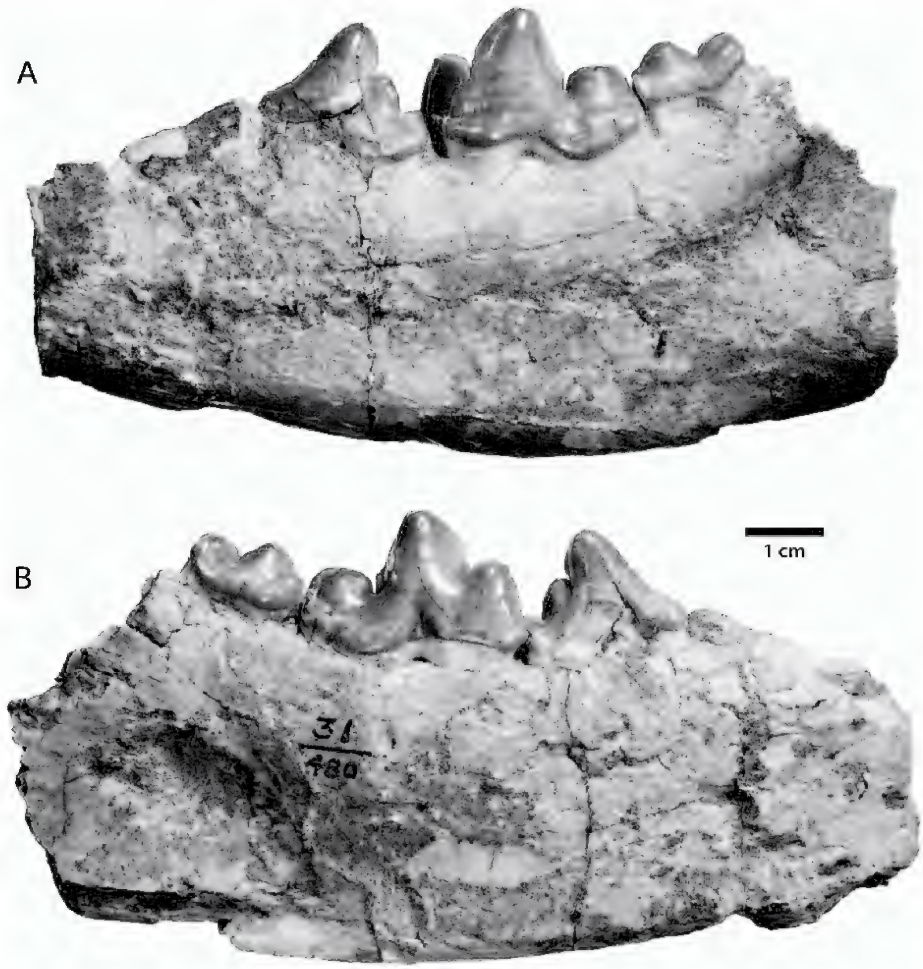


Fig. 22. Holotype mandible of *Rudiocyon amplidens* (LACM 480), with left p4–m2, probably from 1.5 mi south of the Johnson Ranch, from gray beds exposed on the east side of Rudio Creek, Kimberly Member, John Day Formation, Grant Co., Oregon. **A,** labial and **B,** lingual views. This is the largest John Day temnocyonine.

ETYMOLOGY: From the Latin, *amplus*, "large," and *dens*, "tooth," in reference to the robust teeth in this species, the largest of the John Day temnocyonine beardogs.

DIAGNOSIS: Largest John Day temnocyonine species, m1 length, 28.7 mm, m1 without metaconid thereby distinguished from *Temnocyon*; m1 hypoconid centrally placed on talonid, no entoconid; m1 labial cingulum sinuous, not straight as in *Delotrochanter*; p4 narrower than in *Delotrochanter* and *Mammacyon ferocior* but similar in this respect to *M. obtusidens*, *T. ferox*, and *T. macrogenys*. Relatively short m2 (E/F ratio, ~1.9, the highest value for any temnocyonine), not elongate as in *Mammacyon*, with blunt protoconid and hypoconid the principal cusps, aligned one behind the other along the midline of m2; small m2 paraconid occupies anterointernal corner; no metaconid or entoconid. Mandible deep below m1–2 (43 mm), more so than in any other John Day temnocyonine.

REFERRED SPECIMENS: None.

DESCRIPTION: The partial mandible (length, ~114 mm) retains p4–m2. The dorsal border of the jaw is damaged anterior to p4 but has alveoli for p3. Depth of mandible: ~36 mm below p3; 37 mm below the posterior root of p4; 40 mm below the m1

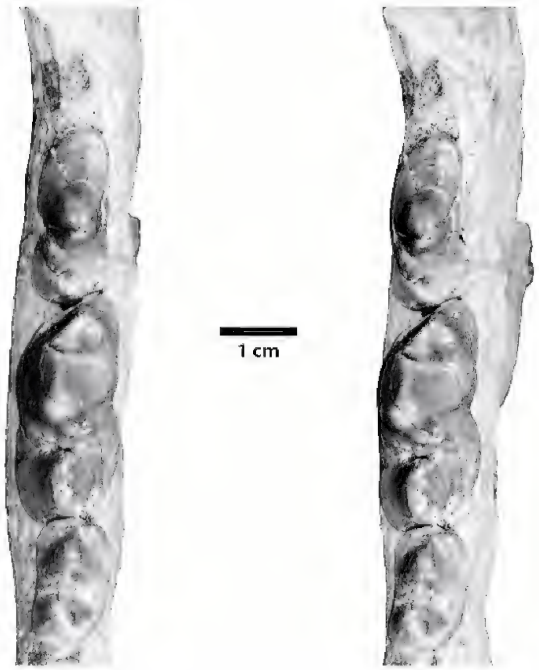


Fig. 23. Occlusal stereopair of the holotype dentition (p4–m2) of *Rudiocyon amplidens* (LACM 480). Note absence of m1 and m2 metaconids and narrow compressed p4.

protoconid; and 43 mm below the anterior root of m2; the anterior masseteric fossa is present below the m2 talonid.

The p4 is narrow and similar in form to the p4 of *Mammacyon obtusidens* and Eyerman's type of *T. ferox*. The tooth is tall, the principal cusp 5 mm higher than the m1 paraconid. A fine enamel ridge on the anterior slope intersects the cingulum. A large labially situated posterior accessory cusp occurs above a small basal cusp. The anterior (8.1 mm) and posterior (10.0 mm) widths of p4 demonstrate a narrow p4 in *Rudiocyon*, which compares with these p4 widths of *M. obtusidens* (7.4, 9.7 mm).

The m1 measures 28.7 mm in length, 13.2 mm in width at the base of the protoconid, 11.8 mm in talonid width, and lacks both a metaconid and entoconid. This is a massive carnassial, the protoconid much taller than the flanking paraconid and hypoconid. The hypoconid is as large as the paraconid and nearly equal in height, indicating the important role played by this pestlelike cusp in crushing. It occupies the center of the talonid, rather than the more labial placement seen in *T. macrogenys*. Anterior to the blunt hypoconid is a small vertical swelling of enamel on the posterior face of the protoconid. It measures 2.4 mm in width, 3.7 mm in height. Above and lingual to this swelling is a thin enamel ridge also situated on the posterior face of the protoconid. This is not a vestige of the metaconid but rather a remnant of a thin protoconid crest that in a plesiomophic m1 forms an incisure with the metaconid. It remains as a low narrow ridge in temnocyonines that have recently lost the metaconid, and is absent in species that have long been without this cusp. A sinuous (not straight as in *Delotrochanter*) cingulum surrounds the base of the tooth on the labial side and on the posterior half of the lingual side, but is indistinct on the lingual side of the trigonid. The lingual cingulum medial to the hypoconid contains a small notch.

The m2 is not elongate and narrows posteriorly, differing from *Mammacyon*: greatest trigonid width is 9.1 mm, talonid width 8.4 mm. The protoconid and smaller hypoconid, both blunt crushing cusps, are anteroposteriorly aligned with the m1 hypoconid. There is variation in the cusp placement of right and left m2: the left m2 shows these two cusps centrally placed, whereas the right m2 shows them closer to the labial margin—it is possible that the latter tooth represents another individual. There is no m2 metaconid or entoconid. However, as in other large temnocyonine species, the anterolabial cingulum of the m2 trigonid is protuberant.

The right P4 protocone, the only remnant of the upper dentition, is similar in size and blunt conical form to that cusp in large species of *Mammacyon*. It measures 10.9 mm in anteroposterior width and compares closely with the protocone of ACM 34–41, the holotype of *M. obtusidens*. The protocone was encircled by a thickened cingulum.

DISCUSSION: *Rudiocyon amplidens* is a carnivore about the same size as *Mammacyon ferocior* or *Delotrochanter oryktes*, and is somewhat smaller than *T. macrogenys*. Thus, the species was one of the larger North American temnocyonines. The m1/m2 length ratio of *R. amplidens* (~1.9) distinguishes it

from *M. ferocior* (1.6), *T. macrogenys* (~1.6), and the species of *Delotrochanter* (~1.6–1.7). In addition, its p4 is not as broad as the *M. ferocior* p4, nor does it have an m1 metaconid as in *T. macrogenys*. *Delotrochanter oryktes* and *D. major* also differ from *R. amplidens* in having a short, posteriorly wide p4 in contrast to the more narrow p4 of *Rudiocyon*.

In its p4–m1, in the form of the mandible, but particularly the P4 protocone, *R. amplidens* shows an evident similarity to *Mammacyon*. However, *M. obtusidens* has a longer m2 and a much smaller m1 than *R. amplidens*, and *M. ferocior* has a boader p4 and a much more elongate m2.

Mammacyon mandibular dentitions are distinguished by the elongate m2 and are known only from the Arikareean of the Great Plains. Because the only evidence of *Mammacyon* in the John Day basin is a maxilla (LACM 5386) from Haystack Valley, the nature of m2 in that species cannot be determined. *T. altigenis* is the only temnocyonine where m2 variation can be estimated and the fossils are not from a single stratigraphic horizon. The variation in m2 length in the *T. altigenis* sample indicates that the hypodigm has a range of 1.67–1.83 for the m1/m2 length ratio (table 6). Yet the difference between the m1/m2 length ratio of *R. amplidens* (1.89) and those of *M. obtusidens–M. ferocior* (1.57–1.6) exceeds that range. LACM 480 cannot be included in *Mammacyon* unless the genus is more broadly defined to include more pronounced variation in dental proportions, particularly with regard to m2.

A partial braincase accompanies the lower jaw and presumably was collected with it. It is remarkable how similar most temnocyonine skulls are in braincase width, a proxy for volume of the cranial cavity (table 7): five of the larger species all measure from 62 to 67 mm, *R. amplidens* among them. The braincase of LACM 480 cannot be compared with temnocyonines with inflated frontal paranasal sinuses because the frontal region anterior to the braincase was not preserved.

The p4–m2 of *Rudiocyon* shows similarities to these same teeth in *T. ferox*. These include the squared posterior heel and cusp pattern of p4; the form of m1, which suggests that the reduced metaconid in *T. ferox* could have finally been lost in LACM 480; and the occlusal form of the relatively short m2 in both species. LACM 480 came from gray tuffaceous sandstone of the Kimberly Member along Rudio Creek a short distance above a supposed correlative ash of the Deep Creek tuff, dated elsewhere at ~27.9 Ma. If this age for the Rudio Creek ash is correct, it would appear to be a much older carnivore than *T. ferox*, which is a smaller and possibly much younger species, and in this case an ancestor-descendant relationship would be unlikely. However, if the correlative ash along Rudio Creek, identified by Fisher (Fisher and Rensberger, 1972: 14) as the Deep Creek tuff in fact represents a much younger undated ash-fall event, then the relative ages of *R. amplidens* and *T. ferox* are unspecified.

Mammacyon Loomis, 1936

TYPE SPECIES: *Mammacyon obtusidens* Loomis, 1936.

INCLUDED SPECIES: *Mammacyon obtusidens* Loomis, 1936; *M. ferocior*, new species.

DISTRIBUTION: Early Arikareean of Oregon; early to mid-Arikareean of South Dakota; mid- or early late Arikareean of southeastern Wyoming.

DIAGNOSIS: Distinguished from *Temnocyon* by absence of the m1 metaconid and different M1 and P4 proportions (table 6, ratios A/B, C/D); from *Temnocyon*, *Rudiocyon*, and *Delotrochanter* by a more elongate m2 (ratio E/F); and from *Delotrochanter* by M1 proportions (ratio A/B), by P3/p3 without posterior accessory cusp, by p4 with labially (not centrally) placed posterior accessory cusp, by a sinuous (not straight) labial cingulum on m1, and by proportions of p2–4 (short broad p2–3 in *Delotrochanter*, longer narrow p2–3 in *Mammacyon*). *Mammacyon* evolves the most extreme form of crushing P4–M1 of the subfamily. See tables 1–5.

DISCUSSION: The genus includes temnocyonines that abandon the plesiomorphic form of the cheek teeth and adopt a durophagous crushing dentition involving not only premolars but also the carnassial-molar battery. The large *Mammacyon ferocior* apparently evolved from the somewhat smaller *M. obtusidens*, both species repre-

sented by skulls and some postcrania. The genus seems restricted to the Oligocene and ranges in time from the early to mid-Arikareean, possibly continuing into the early late Arikareean but is not known in early Miocene faunas.

Mammacyon obtusidens Loomis, 1936
Figures 24–27, 67

Mammacyon obtusidens Loomis, 1936: 44–47, fig. 1.
Mammacyon obtusidens: Macdonald, 1963: 219.
Mammacyon obtusidens: Macdonald, 1970: 63.
Temnocyon percussor: Macdonald, 1970: 61–62.

TYPE: As given in Loomis (1936: 44), but modified as follows: skull with well-preserved basicranium and dentition, axis vertebra, humerus, radius, both ulnae, four metapodials, tibia, partial scapula, two isolated canines, and an astragalus (ACM 34–41), found "in the summer of 1934 in the lower Miocene Rosebud formation on Porcupine Creek, South Dakota, just above the concretionary layer, or about 100 feet above the base of the beds." Additional information is found in Macdonald (1963: 157, 219) as to the type locality, "Amherst College Museum Rosebud 2, Monroe Creek Formation or Harrison Formation." The locality producing the holotype is in the lower Arikaree Group and is of Oligocene age.

DISTRIBUTION: Early to mid-Arikareean: lower Arikaree Group, Wounded Knee area, ACM Rosebud 2, Shannon County, South Dakota; lower Arikaree Group, LACM loc. 1964, Wounded Knee area, Shannon County, South Dakota; John Day Formation, CIT loc. 29, Wheeler County, Oregon.

DIAGNOSIS: Distinguished from *M. ferocior* by smaller size of cranium (basilar length: *M. obtusidens*, 25.5 cm; *M. ferocior*, 28 cm, table 7), postcrania, and mandibular dentition (toothrow length, ~98 vs. 120 mm, table 2), including m1–m2 lengths (*M. obtusidens*, 24.4, 15.5 mm; *M. ferocior*, 27.7, 17.3 mm) and by a much narrower p3–4 width in *M. obtusidens*. The two species differ in P4 and M1 dental ratios A/B and C/D (table 6).

REFERRED SPECIMENS: (1) LACM 9194, left mandible with canine, p1 alveolus, p2–m2, m3 alveolus, isolated right lower canine, right mandibular fragment with m1 talonid and m2 roots, right mandibular fragment with anterior root of p4 and its posterior alveolus, from LACM loc. 1964, Wounded Knee area, "Monroe Creek Formation," NW4, NW4, sec. 3, T39N, R42W, Shannon County, South Dakota, collected by H. Garbani, June 30, 1964; (2) LACM 5386, partial maxilla with P4–M1, from the John Day Formation, CIT loc. 29, "from a large exposure of green beds on north side of Haystack Valley, Wheeler Co., Oregon."

DESCRIPTION: ACM 34–41—Loomis (1936) only briefly described the upper dentition of this fine skull, and did not mention the well-preserved basicranium. It is one of only three temnocyonine skulls in which some part of the auditory bulla is preserved, in this case a crescentic anterior portion formed largely or entirely by the ectotympanic (see Basicranial Anatomy).

The left maxilla retains the canine, P2–M2; on the right, I3, P2–M2. An alveolus for a single-rooted P1 is present on the right, but other alveoli are distorted.

The upper canine, blunted at the tip from wear, measures ~45 mm in length from the tip to the enamel base on the labial face. There is no evident wear groove produced by the lower canine. At the enamel base the canine measures 22.1 mm in anteroposterior length and 14.1 mm in width.

The alveolus of P1 measures 8.7 mm in length, 5.4 in width, and has been slightly distorted by crushing.

P2 measures 18.5 mm in length, the width anterior to the main cusp is 6.8 mm, and the width posterior to this cusp is 7.7 mm. A long posterior slope descends from the main cusp in contrast to the shorter anterior face, both devoid of accessory or cingular cusps. On all upper teeth the cingula are slightly developed basal swellings without sharp or distinct edges. On both P2 and P3 a weak, thin, enamel ridge runs from the main cusp anterolinguad to the cingulum on the anterior slope, and a similar ridge on the posterior slope runs to the posterolabial cingulum.

P3 is an enlarged version of P2, measuring 20.3 mm in length; width anterior to main cusp, 8.2 mm; width posterior to this cusp, 10.6 mm. P3 is somewhat more robust than P2 and much more expanded at its base posterior to the main cusp. There are no accessory or cingular cusps. The anterior and

Fig. 24. Holotype rostrum of *Mammacyon obtusidens* (ACM 34-41) with right I3, P2–M2, left C, P2–M2, from the lower Arikaree Group, Porcupine Creek, Shannon Co., South Dakota. This is one of the earliest durophagous temnocyonines. Focal point of the crushing dentition is centered on the P4–M1 pair. See figs. 67, 69.

Fig. 25. Referred mandible of *Mammacyon obtusidens* (LACM 9194) with left canine, p2–m2, LACM loc. 1964, lower Arikaree Group, Wounded Knee area, Shannon Co., South Dakota. **A,** labial and **B,** lingual views.

posterior faces of P3 are more nearly equal in length, and the tip of the main cusp shows flat apical wear.

P4 is a robust, massive tooth; *M. obtusidens* is the first of the larger temnocyonines to develop this crushing carnassial. P4 has a short metastylar blade, an anteroposteriorly elongate stout paracone, and a greatly enlarged protocone that crushes against the p4 heel. Shear is still accomplished to some degree by the lingual surfaces of the paracone and metastylar blade. The metastylar blade is directed outward at a 50° angle from the anteroposterior axis of the paracone. The blade measures 10.5 mm in length; the paracone measures 18.4 mm from the carnassial notch to its anterior base. A weak enamel ridge runs down the anterointernal face of the paracone to end in a tiny cingular cusp. Directly lingual to the paracone is the

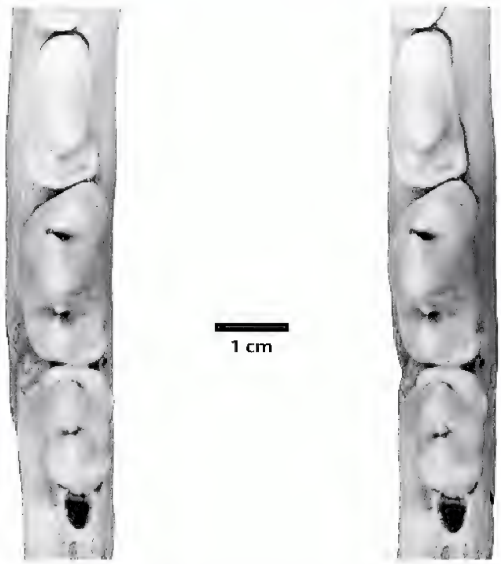


Fig. 26. Occlusal stereopair of the mandibular dentition (p4–m2) of *Mammacyon obtusidens* (LACM 9194). Note absence of m1 and m2 metaconids.

blunt, knoblike protocone: the protocone is separated from the paracone by a broad valley. Anteroposterior length of the protocone is 11 mm; greatest width of P4 at the level of the protocone is 21.5 mm. Only a narrow embrasure (~7 mm in length) remains between P4 and M1 to receive the trigonid of m1, and a similarly reduced space also occurs in *M. ferocior*.

M1 measures 20.4 mm in length, 28.2 mm in width. In *M. obtusidens* the tooth comprises a labial part dominated by the para- and metacone, and an enlarged lingual half created by swelling of the lingual cingulum around the broad protocone region. Between the lingual and labial parts of the tooth is a prominent constriction, giving the tooth a "waist" at the level of the protocone basin. The paracone is somewhat larger than the metacone; the parastyle, swollen labially and ventrally downturned, is more pronounced than the metastyle. Here, as in other large temnocyonines, M1 has a "folded" appearance as if the entire labial half were inwardly rotated toward the lingual half about an anteroposterior axis through the protocone basin. The protocone is centrally situated in a flat expanse of enamel. A preprotocrista runs from the protocone to the anterior cingulum but there is no postprotocrista nor para- and metaconules. A heavy swollen lingual cingulum, about equally developed throughout its extent, surrounds the protocone region.

M2 measures 10.5 mm in length, 17.9 mm in width. It is much smaller than M1 and fits into the concavity on the posterior margin of the larger molar. The paracone is much larger than the abbreviated metacone, but only slightly taller. The stylar shelf and labial cingulum external to the paracone are better developed than these features labial to the metacone as a result of the reduction of the metacone. The protocone basin occurs at the constricted "waist" of the tooth, and here also, as for M1, the labial half of M2 is rotated or "folded" inward. The protocone is a small, low blunt cusp protruding from the enamel flat forming the lingual half of the tooth. It is surrounded by a swollen cingulum, which is considerably worn. M3 was absent; there is no alveolus and there is no place on the maxilla posterior to M2 for an M3.

The associated limb and vertebral elements are similar in form to skeletal elements of *Mammacyon ferocior* (F:AM 27562) from north of Keeline, Wyoming. Comparisons of the ulna, humerus, astragalus, and scapula show no differences other than size. The limb elements of *M. ferocior,* in association with its mandible, indicate a species larger than *M. obtusidens* (ACM 34–41).

LACM 9194—Only the complete left mandible is described here; the two isolated jaw fragments and canine only duplicate structure observable in the more complete lower jaw. LACM 9194 was initially described as *Temnocyon percussor* by Macdonald (1970: 61–62).

The jaw is short and massive. Depth under the main cusp of p2 is 38.4 mm, and 35.9 mm below the m1 protoconid. Premolars and molars are large, robust teeth; the molars, especially m2–3, are conspicuously tilted forward on the curvilinear margin of the ascending ramus. The inclined m2–3 are characteristic of temnocyonines, consequently M2 is often dorsally elevated relative to M1 to accommodate this configuration of the lower molars. Such an M2 is present in the holotype (ACM 34-41). The unworn teeth indicate a mature young adult.

The canine is a large, recurved tooth, 38.9 mm in height from tip to enamel base, measured on the labial face. Its anteroposterior width is 19.1 mm measured at the base of the enamel; its labiolingual width is 12.6 mm. A wear groove produced by the upper canine begins near the tip on the posterior surface, continues down the posterior slope, trending slightly labiad, eventually terminating about 9.5 mm above the enamel base on the posterolabial face. Two fine enamel ridges traverse the tooth from tip to enamel base: the first courses down the center of the lingual face, the second traverses the posterolingual face.

The single alveolus for p1, although crushed, measures ~8 mm in length, 6.2 mm in width. Elongation of the large alveolus suggests that the tooth was directed anterolabially.

The p2 measures 14.4 mm in length, 5.8 mm in anterior width, and 6.4 mm in posterior width. There are no accessory or cingular cusps. A fine enamel ridge descends the somewhat steeper anterior face to the anterolingual corner of the tooth, and a similar ridge occupies the posterior face, ending at the posterolabial corner.

The p3 measures 17.7 mm in length, 6.4 mm in anterior width, and 7.8 mm in posterior width. There are no accessory cusps, but there is a small basal cusp situated at the center of the posterior cingulum. A thin enamel ridge descends the anterior face to the anterolingual corner; a second ridge traverses the posterior face to the basal cingulum cusp.

The p4 measures 20.4 mm in length, 7.5 mm in anterior width, and 9.7 mm in posterior width. A large posterior accessory cusp is labially situated half the distance down the posterior slope. A small basal cusp on the posterior cingulum lies below the posterior accessory cusp. A fine enamel ridge follows the anterior slope and ends in the anterolingual corner as in p2–3, but a posterior ridge is largely obscured by development of the large posterior accessory cusp.

The bases of P3 and p3–4 are posteriorly widened but this is less pronounced relative to *M. ferocior* or *D. oryktes* teeth where such widening of the posterior base is strongly developed.

The m1 measures 24.4 mm in length, 11.4 mm in posterior trigonid width, and 10.9 mm in greatest talonid width. Trigonid length is 17.4 mm. This is a robust, short, blunt-cusped carnassial that has lost the metaconid, although a small wear facet on the labial face of the protoconid shows that paraconid-protoconid shear is retained. The short, swollen paraconid blade is angled inward and is much lower in height than the principal cusp of p4. The protoconid is compressed to form a blade running forward and downward to form the incisure with the paraconid. A short enamel ridge 4 mm in length descends the posterior surface of the protoconid to form the incisure with the hypoconid, a massive blunt cusp placed directly behind the protoconid and centrally situated on the talonid. There is also a low enamel swelling on the posterolingual wall of the protoconid that represents the vestige of the incisure once shared with the metaconid. Its presence indicates that the metaconid has probably been lost relatively recently in this lineage. There is no entoconid. The m1 has a swollen, weakly differentiated cingulum, most evident on the labial side where it is sinuous: it rises below the protoconid, descends at the protoconid-hypoconid incisure, and rises again beneath the hypoconid (in contrast, the labial m1 cingulum is straight in *Delotrochanter*). At the posterolingual corner of the m1 talonid, the cingulum is slightly enlarged, creating a marked indentation of the cingulum anterior to this swelling (also found in *M. ferocior*).

The elongate m2 is diagnostic of the *Mammacyon* lineage in the Great Plains. Its length is 15.5 mm; greatest trigonid width, 9.6 mm; greatest talonid width, 8.7 mm: m2 has a rectangular occlusal outline. The labially placed protoconid is the largest cusp. There is no metaconid but a small, distinct paraconid occupies the anterolingual corner of m2. The only talonid cusp is a low, blunt, somewhat labially situated hypoconid. There is no entoconid. The pronounced inclination of m2 (and m3) on the edge of the ascending ramus of the mandible, tilted forward nearly 30° from the horizontal, further emphasizes the short toothrow and massive quality of the teeth.

The m3 is represented by a single alveolus, length 4.7 mm, width 4.1 mm, placed close against the posterior edge of m2.

Length of the toothrow from p2–m2 is 86.2 mm; from the base of the enamel on the

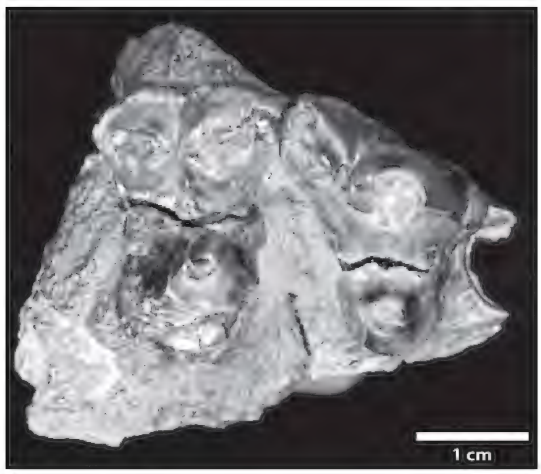


Fig. 27. Referred maxilla of *Mammacyon obtusidens* (LACM 5386) with right P4–M1, Turtle Cove Member, John Day Formation, Haystack Valley, Wheeler Co., Oregon. Note apical wear on all cusps, indicating crushing action of P4–M1.

posterior face of the canine to the anterior rim of m3 alveolus is 98.3 mm; from anterior rim of p1 alveolus to posterior rim of m3 alveolus is ~99 mm.

LACM 5386—I refer to *M. obtusidens* a partial maxilla with right P4–M1 and the alveolus for the posterior root of P3, from CIT Locality 29, Haystack Valley, Wheeler County, Oregon. It was found among unidentified material in the collection of the Los Angeles County Museum and has not been previously described. The teeth are most similar in form to ACM 34-41 (*M. obtusidens*) and F:AM 54134 (*M. ferocior*). This is the only specimen from the John Day beds assigned to *Mammacyon*; it represents a smaller individual than the holotype of *M. obtusidens* and is closer in size to LACM 9194.

The alveolus (greatest width, 8.2 mm) for the posterior root of P3 is very large, indicating a posteriorly broad premolar at least 9 mm in width. This alveolus indicates that P3 was closely set against the base of P4 as in the holotype.

P4 measures 21.8 mm in length, 18.2 mm in greatest width, and is characterized by the short yet robust metastylar blade relative to the large paracone and protocone. Metastylar blade length is 8.1 mm; width of the blade is 7.4 mm. The upper carnassial is nearly as wide as long, and shows blunted cusps with pronounced apical wear (there is only a weak vertical shear facet on the lingual face of the paracone-metastylar blade). The enormous protocone is responsible for the width of P4: it extends as far toward the midline of the palate as does the M1. An enlarged protocone is characteristic of *Mammacyon;* in *Delotrochanter* the P4 protocone does not extend as far toward the midline. A slightly swollen cingulum surrounds P4, and is somewhat more defined around the base of the metastylar blade than elsewhere on the tooth. A conspicuous valley separates the large blunted paracone from the much lower knoblike protocone.

M1 measures 17.8 mm in length, 24.8 mm estimated transverse width (the anterolingual cingulum is broken), and 13.1 mm in anteroposterior width of the protocone region. The form of the tooth is comparable to M1 of ACM 34-41. The embrasure for m1 between P4 and M1 is much reduced as in the holotype, thus there was probably no m1 metaconid. In addition, the M1 of LACM 5386 shows the "folded" appearance in which the labial half of the tooth is rotated inward toward the lingual half as in ACM 34-41. The knoblike protocone of M1 was isolated within the broadened protocone region and surrounded by a swollen lingual cingulum; a weak preprotocrista runs from protocone toward the anterior cingulum but no postprotocrista is apparent. Paracone, metacone, and protocone of M1 are blunt cusps with flat apical wear surfaces. The paracone and metacone were once tall cusps but wear has reduced their height so that evidence of vertical shear on their lingual faces is equivocal. In mature individuals mastication emphasized the processing of hard food items, also suggested by the blunt, knoblike protocones of both M1 and P4.

A vestige of the labial M2 alveolus indicates that the tooth was small and fitted tightly against the posterior margin of M1 in the same location as the holotype.

DISCUSSION: *Mammacyon obtusidens* is the oldest species that can be confidently attributed to the genus. The maxilla (LACM 5386) from the John Day Formation of Haystack Valley, Oregon, can be conservatively dated

at younger than 28.7 Ma based on its probable site of collection close above the Picture Gorge ignimbrite; an age estimate for the locality falls in the interval from ~28 to 28.7 Ma. The first appearance of *M. obtusidens* in the Great Plains is based on the referred mandible (LACM 9194) from the "Monroe Creek Formation" of the Wounded Knee area in southwestern South Dakota. The holotype cranium and associated postcranials (ACM 34-41) were attributed to the "Monroe Creek or Harrison Formation" and are also part of the Wounded Knee fauna of Macdonald (1963, 1970). However, a reliable correlation of these rock units with the type Monroe Creek and Harrison formations of Hatcher (1902a) north of the town of Harrison in northwest Nebraska has not been established, and the mammalian fauna from the "Monroe Creek" and "Harrison" of the Wounded Knee area lacks age-diagnostic species found in the stratotype Harrison Formation in Sioux County. The Wounded Knee fauna from the "Monroe Creek-Harrison" interval in South Dakota is an early to mid-Arikareean fauna (see Age and Correlation), hence the holotype of *M. obtusidens* is assigned to the late Oligocene — the species had attained the specialized durophagous dental traits typical of the genus at least by the earlier late Oligocene, and this dental trend continued in the Great Plains with *M. ferocior*.

The *M. obtusidens* mandible (LACM 9194) is from the same Wounded Knee locality as the canid *Enhydrocyon pahinsintewakpa*, the most plesiomorphic species of its genus (Wang, 1994: 90); this locality (LACM 1964) occurs near the base of the "Monroe Creek" unit and in close proximity to the Sharps Formation, which includes leptauchenine oreodonts in the same area (Macdonald, 1963: 162). These mammals document an early Arikareean age for the stratigraphic level that yielded the mandible of *M. obtusidens*.

This conclusion is supported by the stratigraphic position of the descendant of *M. obtusidens*, the larger terminal species of the lineage, *M. ferocior*. *Mammacyon ferocior* from the Pine Ridge of Niobrara County, north of Keeline, Wyoming, is a species of larger size in which derived dental features of the *M. obtusidens* holotype become further accentuated. Thus, in *M. ferocior* the teeth are similar in form but larger, more massive, with even greater emphasis on the crushing function of the cheek teeth. The fauna from north of Keeline is considered here to be intermediate in age between the Wounded Knee "Monroe Creek" fauna and the fauna of the stratotype Harrison Formation in northwest Nebraska.

The mandibular fragment (LACM 15908) attributed in this study to cf. *Mammacyon* from the Sharps Formation of South Dakota was collected stratigraphically below and ~4 mi (6.4 km) north of the locality that produced the referred *M. obtusidens* mandible (LACM 9194). It possibly represents the earliest record of *Mammacyon* in the Great Plains. It has reduced the m1 metaconid to a vestigial remnant and shows the robust teeth and thick mandible that would be expected in the ancestor of *M. obtusidens*. However, LACM 15908 lacks the elongate m2 relative to m1 (m1/m2 length ratio, ~1.7) common to *M. obtusidens* and *M. ferocior* and is too incomplete to permit confident referral to the genus. The m2 protoconid and hypoconid are centrally situated, a character of *Mammacyon* and *Delotrochanter*; these cusps are labially placed in *Temnocyon*.

Mammacyon ferocior, new species
Figures 28–31

TYPE: Right partial mandible with i3 root, c–m3, and associated limb elements and vertebrae: atlas, caudal vertebra, sacrum, glenoid of scapula, left humerus, distal right humerus, both ulnae, rib fragments, left metacarpal 2, proximal left and right metacarpal 3, innominate fragments, partial left femur, left tibia, proximal right tibia, both calcanea, left astragalus, proximal right astragalus, right navicular, both cuboids, left ectocuneiform, right metatarsal 2, left distal metatarsal 3, proximal right metatarsal 5 (reduced), from ?Harrison Formation, north of Keeline, Niobrara County, Wyoming, collected by Charles Falkenbach, 1931 (F:AM 27562).

DISTRIBUTION: Mid- or early late Arikareean, Arikaree Group, Niobrara County, Wyoming.

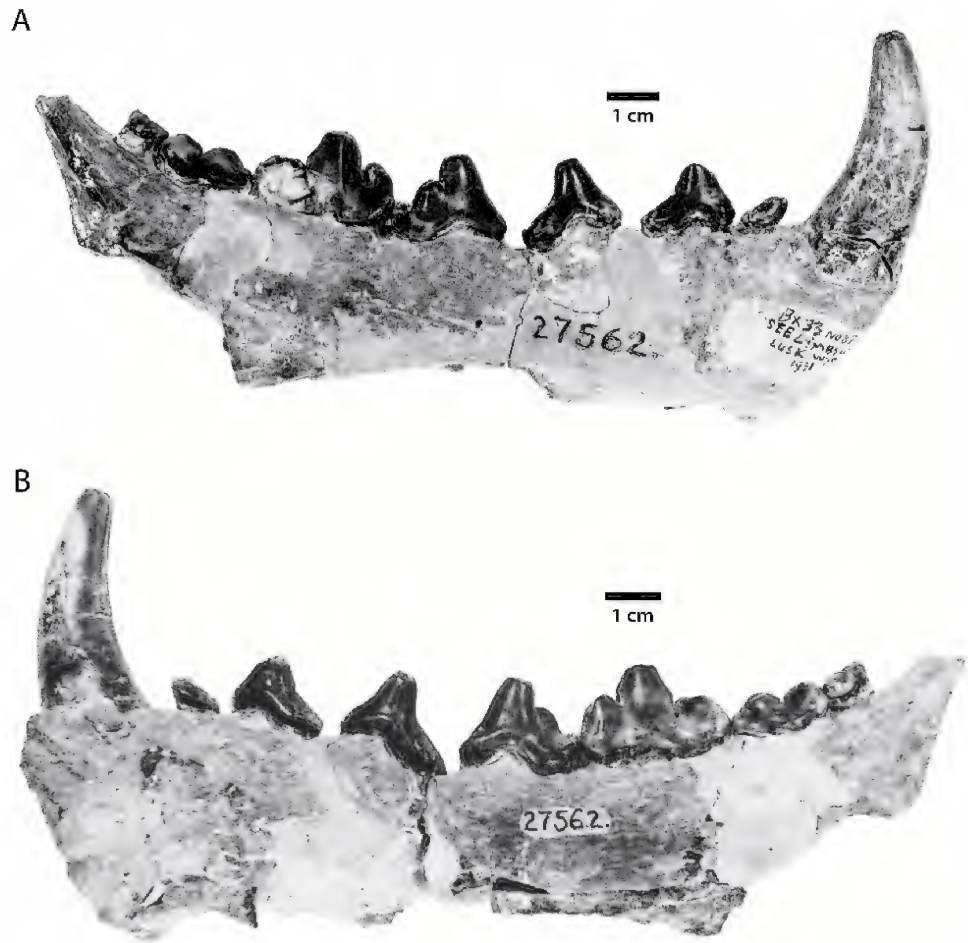


Fig. 28. Holotype mandible of *Mammacyon ferocior* (F:AM 27562) with right canine, p1–m3, from the Arikaree Group, north of Keeline, Niobrara Co., Wyoming. The large crushing p4 nearly equals the carnassial in size. **A,** labial and **B,** lingual views.

ETYMOLOGY: From the Latin, *ferocior*, "particularly fierce," in allusion to the large size and presumed disposition of this predator.

DIAGNOSIS: Largest species of the *Mammacyon* lineage, thus sharing the same dental characters of form and proportion as *M. obtusidens* but distinguished by larger size. Dental ratio A/B, 1.23; ratio C/D, 1.13 (table 6), lower than all *Temnocyon* species. Ratio C/D (1.13), lowest of all temnocyonines. Distinguished from other large temnocyonines such as *R. amplidens* by an elongate m2 (ratio E/F: 1.6 in *M. ferocior*, ~1.9 in *R. amplidens*); from *T. ferox, T. percussor*, *T. fingeruti*, and *T. macrogenys* by absence of the m1 metaconid; from *T. macrogenys* by much smaller size; and from *Delotrochanter oryktes* and *D. major* by a p4 with labially placed posterior accessory cusp (centrally placed in *Delotrochanter*). *M. ferocior* p4 posteriorly broader than in *M. obtusidens*. Cranium with greatly inflated frontal sinuses relative to small braincase volume (table 7).

REFERRED SPECIMEN: F:AM 54134, a skull with poorly preserved basicranium yet in other features complete and uncrushed. This is the largest known North American temnocyonine skull (basilar length, 28 cm). Upper dentition with alveoli for six incisors, two canines, left P1–3, right P2–3; complete right P1, P4–M2 (P4 damaged), and left P4–M2; M3 not present in the species. From the ?Harrison Formation, north of Keeline, Niobrara County,

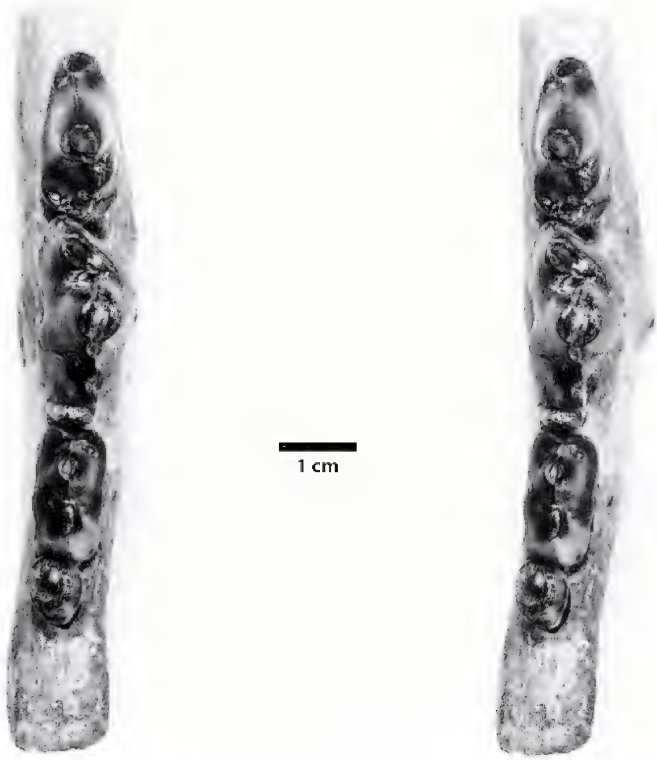


Fig. 29. Occlusal stereopair of the mandibular dentition (p4–m3) of *Mammacyon ferocior* (F:AM 27562). Note absence of m1 and m2 metaconids, apical wear on p4–m2 cusps, a labial shear facet on m1 protoconid-paraconid, and the broad p4 (compare fig. 23).

collected by C. Falkenbach in 1944, from a stratigraphic level "high in the formation" in this area.

DESCRIPTION: FAM 27562—The depth of the mandible (estimated at ~44 mm) is uncertain because the ventral border of the horizontal ramus is damaged. Length of toothrow from the posterior border of the canine alveolus to the posterior limit of m3 is 126.2 mm. The mandibular symphysis extends from the anterior canine border almost to the posterior border of p2, having a greatest length of 48.8 mm and depth of 36.3 mm.

Lower canine height is 47.5 mm above the labial alveolar border. The tooth is grooved on its posterolabial face by the upper canine, identical to the similarly positioned groove in LACM 9194 (*M. obtusidens*). At the enamel base the canine measures 14 mm in width, 20.3 mm in anteroposterior length, and is somewhat posteriorly recurved. In addition to the groove worn by the upper canine, there is a deep elliptical wear facet on the anterolingual face produced by the I3 which is much larger than I1–2 based on alveolar dimensions.

The p1 is a small, peglike tooth that measures 9 mm in length, 5.9 mm in width. The main cusp is anteriorly placed as in all temnocyonines, with a long posterior slope and no accessory or cingular cusps.

The p2 is much larger than p1, measuring 17.9 mm in length, 8.1 mm in greatest width posterior to the main cusp. There are no accessory or cingular cusps. The posterior face is longer and more gently inclined relative to the more vertical anterior face. Fine enamel ridges are present on both anterior and posterior faces and, as in *M. obtusidens*, the anterior ridge descends to the anterolingual cingulum whereas the posterior ridge runs to the posterolabial cingulum. The tooth itself is angled outward; that is, the

anterior p2 root is more labial in position than the posterior root. A somewhat swollen cingulum is more defined along the lingual bases of p2, p3, and p4 relative to its less pronounced labial expression.

The p3 is simply a taller, larger example of p2; it measures 19.3 mm in length, 9 mm in width. There are no accessory or cingular cusps despite the broadened heel of p3 relative to p2. Thin enamel ridges run down the anterior and posterior faces to the barely discernible cingulum, the anterior ridge contacting the anterolingual corner, the posterior touching the posterolabial corner where the cingulum is better developed along the posterior margin.

The p4 is more massive and robust than p3. It measures 21.9 mm in length, 10.7 mm in width. A large posterior accessory cusp occurs about halfway between the tip of the main cusp and the crown base. It lies labial not only to the main cusp but also to the basal cusp occupying the center of the broad posterior shelf of p4. The main cusp of p4 is nearly as tall and robust as the protoconid of m1. Both p3 and p4 are particularly tall premolars; their principal cusps are each ~4 mm taller than the m1 paraconid.

Flat apical wear facets are present on the principal cusps of p1–4 and on the m1 protoconid.

The m1 measures 27.7 mm in length, ~13 mm in width (the labial talonid is lost). The carnassial is large and robust yet appears rather low and almost dwarfed relative to the tall, massive premolars. The metaconid is absent. Both protoconid and paraconid are massive, broad cusps, the protoconid showing strong apical wear. However, carnassial shear is evidenced by a near-vertical facet on the labial face of the paraconid-protoconid. The paraconid, placed anterolingual to the protoconid, has not rotated into a position directly anterior to the protoconid as in carnivorans with highly developed carnassial shear. The hypoconid is large, blunt, centrally placed on the talonid, and the entoconid is absent. The cingulum is not well defined and appears only as a vague swelling around the base of the tooth. However, a prominent swelling of the enamel occurs at the posterolingual corner of m1 and represents a small cingular shelf; anterior to this swelling on the lingual margin of the talonid, the base of m1 is indented or "notched." Both the cingular swelling and indentation also occur in *M. obtusidens*.

The m2 measures 17.3 mm in length, 10.3 mm in width. This is the longest North American temnocyonine m2, yet the m1 of this same individual is exceeded in length by the m1 of three other species (*T. macrogenys*, *D. oryktes*, *R. amplidens*). A low, blunt protoconid occupies the center of the trigonid; a hypoconid of nearly equal height lies directly behind the protoconid in the center of the talonid. There is neither metaconid nor entoconid. A vestigial paraconid appears as a low platform at the anterolingual corner of m2.

The m3 is a small, oval tooth with minimal surface relief. It measures 8.6 mm in length, 7.2 mm in width. Because the enamel is damaged, cusp pattern is uncertain; however, a low protoconid was the principal cusp and a small, reduced talonid is present.

FAM 54134—The skull is largely uncrushed and the largest known for the subfamily. It displays "bearlike" proportions reflected in the swollen muzzle, inflated frontal region, heavy zygomatic arches, and pronounced sagittal and lambdoid crests. The upper teeth represent the most highly specialized durophagous dentition developed by a temnocyonine, a crushing dentition unlike that of bears (Ursinae). The locus of crushing in the upper teeth of F:AM 54134 involves P3–M1/p4–m2 whereas in living ursine bears the M1–M2/m1–m3 serve this function.

Basilar length of skull is 280 mm comparable in size to adult male *Ursus americanus*. The braincase is proportionately small relative to overall skull size; in fact the expanded frontal sinuses appear to have had a volume greater than the cranial cavity (table 7). The secondary palate is long (14 cm) and narrow for a skull of this length: palatal width measured across the M1s is 8.7 cm whereas only 3 cm of this is occupied by the palatal bone between the teeth, with the remainder taken up by the enlarged molars. The tall, narrow infraorbital foramen (height, 18 mm; width, 9 mm), opens on the maxilla above the upper carnassial. The orbitotemporal region is long: postorbital length is ~19 cm, preorbital ~12.5 cm. The left orbital region

Fig. 30. Cranium of *Mammacyon ferocior* (F:AM 54134) in (**A**) right lateral; (**B**) dorsal; and (**C**; *opposite page*) left lateral (restored) views, from the Arikaree Group, north of Keeline, Niobrara Co., Wyoming, showing (B) width of the frontal paranasal sinuses relative to braincase volume.

preserves the elongate depression in alisphenoid and orbitosphenoid bones for the optic foramen, sphenorbital fissure, and anterior aperture of the alisphenoid canal. The canal is 20 mm in length; its posterior opening shares a common fossa with the foramen ovale. The foramen rotundum opens internally into the canal as in other temnocyonine crania.

The basicranium is foreshortened: the length from the common fossa for the posterior opening of the alisphenoid canal and the foramen ovale to the ventral notch of the foramen magnum (an estimate of basicranial length) is only 5.5 cm, approximately one-fifth the basilar skull length. Although the basicranium is damaged there is an evident similarity to the *M. obtusidens* basicranium (ACM 34-41). Enough of the basicranial axis is preserved to show that, on the right side, the margin of the basioccipital was deeply excavated for an enlarged inferior petrosal venous sinus. This is the most pronounced development of the sinus in any temnocyonine skull and is related to the large size of *M. ferocior*. The sinus includes a deep central pocket also seen in *Temnocyon altigenis* (UCMP 9999), penetrating 13 mm into the basioccipital.

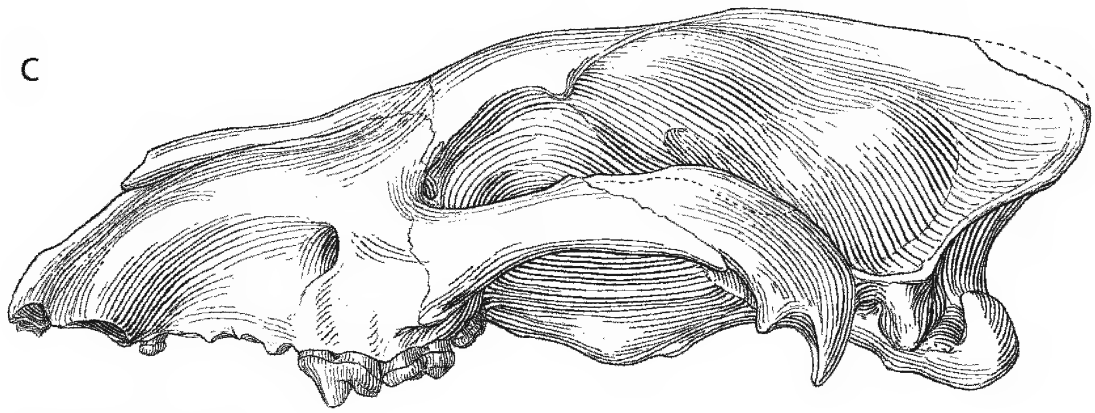


Fig. 30. *Continued.*

The morphology of the upper dentition is comparable to ACM 34-41, however the Keeline skull has larger, more robust teeth, a massive P3–M2 crushing dental battery, close-spaced P2–4 (no diastemata), huge canines, and a full complement of incisors with large I3.

Incisor alveoli show that the upper incisors became larger from I1 to I3: I1 alveolus measures 9.1 mm in length, 4 mm in width; I2 alveolus, 11.2 mm × 6.1 mm; I3 alveolus, 11.5 mm × 10 mm. There is a diastema of ~9 mm between I3 and the canine alveolus. The canine alveolus measures 24 mm × 15 mm; the maxilla surrounding the canine roots is swollen to accommodate the large canines, indicating a male individual.

The upper premolars were somewhat crowded judging from the placement of P1–3 alveoli. This is not the crowding seen in many young amphicyonids since the wear on cheek teeth shows F:AM 54134 to be a mature adult. As is the case in the mandible, P2 is angled outward and shows the effect of crowding more than any other tooth, its posterior alveolus more lingual than the anterior. This degree of crowding also occurs in the upper teeth of *M. obtusidens* (ACM 34-41) and must be characteristic of large species of *Mammacyon*.

P1 is a small rounded peg (7.6 mm in length, 6.4 mm in width) preserved only on the right side close behind the large canine. The alveoli for P2–3 measure 18.6 mm by 9.4 mm, and 21.1 mm by 13.4 mm, respectively. The larger posterior alveolus common to each of these premolars shows that both P2 and P3 were posteriorly broad, especially P3.

The enormous P4 with its short metastylar blade and massive paracone and protocone represents the culmination of the trend toward a crushing dentition within the genus. Its 26 mm length is almost equalled by its 23.1 mm width. Length of the metastylar blade is 10 mm; length of paracone including the parastylar region is 17.4 mm. The embrasure between the protocones of P4 and M1 for the m1 trigonid is reduced to 8.5 mm in anteroposterior length, notably less than the anteroposterior lengths of the protocones themselves (P4 protocone, 12 mm; M1 protocone, 17.4 mm) so that very little of the lower carnassial could have been inserted into this space. Occlusion of the *M. ferocior* mandible (F:AM 27562) with the upper teeth of the skull demonstrates that the m1 protoconid is arrested at the level of the lingual cingulum of M1 by the narrow embrasure; the m1 paraconid and hypoconid also act as enamel stops against P4 and the M1 protocone basin. Thus, although some shear occurred between upper and lower carnassials, particularly in unworn teeth, a specialized crushing action was the dominant occlusal mode. Following an initial shearing stroke as the mandible brought the lower carnassial into contact with the upper teeth, the final phase of occlusion between p4–m2 and P3–M2 must have been mortar and pestle crushing employing the lingually expanded P4–M1 protocones. Ratios A/B and C/D (table 6) are the lowest in the genus, and

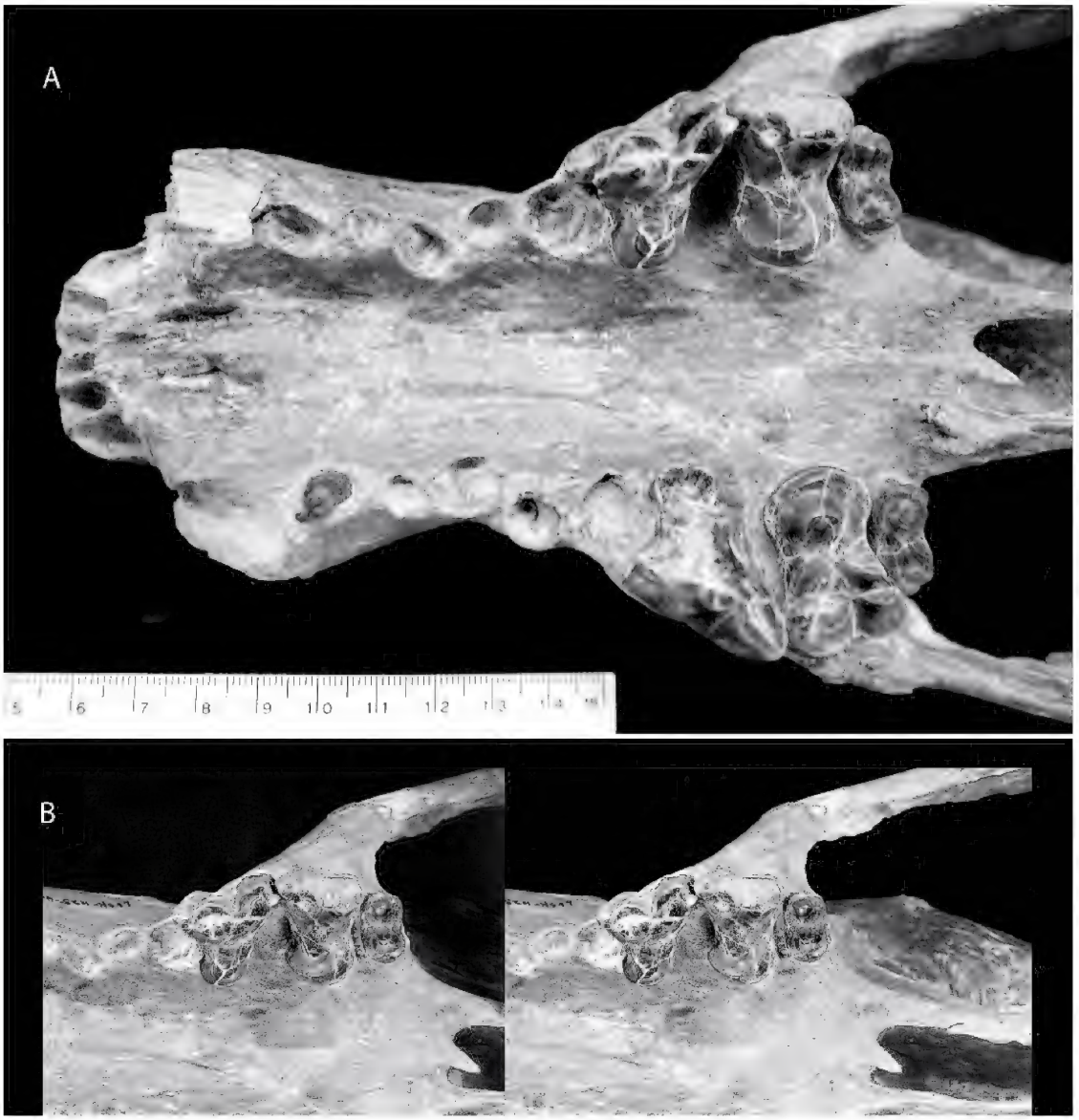


Fig. 31. *Mammacyon ferocior* (F:AM 54134) rostrum (**A**) in palatal view with right and left P4–M2, right P1, and alveoli for I1–3, C, P2–3 , from the Arikaree Group, north of Keeline, Niobrara Co., Wyoming. Stereophotos (**B**) of crushing P4–M2. This is the largest species of *Mammacyon*, and represents the climax of durophagy in the genus.

are related to the development of a crushing occlusion in *M. ferocior*.

M1 measures 21.4 mm in length, 29.8 mm in width. Despite its enormous size, it retains the characteristic temnocyonine configuration in which an expanded protocone region is separated from the enlarged labial half of the tooth by a prominent constriction at the level of the protocone basin. The paracone is slightly larger than the metacone. These two cusps are labially bordered by a cingulum, which is more pronounced labial to the paracone and is continuous with a small parastyle at the anterolabial corner of M1. Although the cusps are worn, in all respects they appear as in *M. obtusidens*. The large

protocone is situated in the center of a broad enamel platform more developed than in any other temnocyonine species. The enamel platform is surrounded by an expanded lingual cingulum. A preprotocrista extends from the protocone toward the anterior cingulum, and a weak vestige of a postprotocrista also appears on the surface of the enamel platform trending toward the posterior cingulum. There are no para- or metaconules. Lateral to the protocone itself is a deep protocone basin that receives the m1 hypoconid much as pestle fits against mortar.

M2 is rectangular in occlusal outline with its long axis oriented transversely; it measures 10.8 mm in length, 17.4 mm in width, and is much smaller than M1. The paracone is much larger than the metacone. A strong labial cingulum borders only the paracone; the metacone cingulum is weak. The paracone-metacone region forms an elevated labial rim that overlooks the flat protocone region. The centrally situated protocone on this enamel flat is but a reduced version of the same cusp on M1. Wear has reduced the protocone to a flat surface nearly coplanar with the enamel flat on which it rests.

M3 was no longer present in this species. The maxilla terminates abruptly behind M2 in smooth bone indicating that in life there was no tooth posterior to M2.

Length of the upper toothrow from the posterior border of the canine alveolus to the posterior border of M2 is 104.2 mm. Length of the left P1–3 based on an alveolar measurement is ~51 mm. Greatest length of P4–M2 is 55.7 mm.

Discussion: Although the mandible (F:AM 27562) and skull (F:AM 54134) here assigned to *Mammacyon ferocior* were not associated, the teeth in the mandible not only correspond in size and form to the upper teeth but also occlude perfectly. The collector, Charles Falkenbach, did not provide exact locality data for these fossils, but we know that they were derived from the same general locality north of Keeline, Wyoming, from gray volcaniclastic fine-grained sandstone of the Arikaree Group. Recent geologic study of the area north of Keeline and examination of the fossils previously collected from the area by the Frick Laboratory suggest that the fauna including *M. ferocior* can be considered as mid- to early late Arikareean in age. The fauna lacks a number of mammalian species that typify the late Arikareean (Ar3) Harrison Formation fauna of Sioux County to the east (see Age and Correlation). Although a radioisotopic age is not available for the *M. ferocior* hypodigm, faunal relationships suggest that the species is older than ~23 Ma. *Mammacyon* has not been found in any known latest Arikareean (Ar4) fauna.

Associated limb elements and vertebrae were collected with the *M. ferocior* mandible (F:AM 27562) in 1931; they are alike in form but larger in size than the postcranials associated with the genoholotype of *Mammacyon* (ACM 34-41). Additional limb and foot bones (F:AM 107758) collected by Falkenbach in 1950 "from brownish sandstone 15 feet below highest exposure, west end, north of Keeline, Wyo." belong to a large temnocyonine and also possibly represent limb elements of *M. ferocior*. Included are a humerus (length, 234 mm; width of distal end, 50.3 mm), partial scapula (only the glenoid and adjacent blade), distal ?tibia, distal ?radius, and two elongate metapodials. *M. ferocior* retained a postcranial skeleton much like (if not identical to) *M. obtusidens*, indicative of a digitigrade cursorial gait in which the forelimb was characterized by a narrow distal humerus, a lengthening of radius and ulna with limited ability for pronation/supination, and an elongate tarsus and carpus (see Postcranial Osteology). These are the first large Cenozoic carnivorans to achieve a limb skeleton modified for a digitigrade stance, restricted fore-aft limb excursion, and a striding cursorial gait. This recommends a behavioral mode in which a cursorial habit was coupled with durophagous feeding, an ecology to some extent paralleling spotted hyaenids (*Crocuta*) in the Old World.

None of the other very large North American temnocyonine species (*Temnocyon macrogenys*, *Delotrochanter major*, *Rudiocyon amplidens*) are known from skulls, although *Delotrochanter oryktes* is represented by a substantial partial cranium (UNSM 47800) from the carnivore dens at Beardog Hill, Agate National Monument. The skull of *M. ferocior* (F:AM 54134) is the most complete cranium of a large temnocyonine and demonstrates that the terminal species of the

Mammacyon lineage possessed a rather ursid-like profile, strong inflation of the frontal sinuses relative to volume of the cranial cavity, a broad rostrum swollen around the large canine alveoli, and a robust dentition with cheek teeth adapted for crushing bone, fibrous sinew, and muscle.

cf. *Mammacyon*
Figure 32

Sunkahetanka pahinsintewakpa (in part): Macdonald, 1970: 60 (LACM 15908 was initially placed in the canid genus *Sunkahetanka*).

REFERRED SPECIMEN: Fragment of mandible with left m1–2, posterior part of p4, and alveolus for m3 (LACM 15908), Sharps Formation, LACM loc. 1872, south of Wolf Ranch, NE1/4, sec. 15, T40N, R42W, Shannon County, South Dakota, collected by J. Harksen, July 1963.

DISTRIBUTION: Early Arikareean, Sharps Formation, Wounded Knee area, South Dakota.

COMMENTS: A small temnocyonine slightly larger than *T. altigenis* and with more derived m1–2; LACM 15908 has a more robust ml (length, 20.5 mm; width, 9.9 mm) relative to the *T. altigenis* hypodigm (m1 length, 17.4–19.5 mm; m1 width, 7.7–9.3 mm); m1 metaconid more reduced relative to *T. altigenis* (metaconid is a small vestigial cusp on posterolingual slope of protoconid); m2 not elongate (m1/m2 length ratio, ~1.7) thus differs from *M. obtusidens–M. ferocior* (m1/m2 length ratios, 1.57, 1.6); m2 protoconid and hypoconid in anteroposterior alignment and more centrally situated than these cusps in *T. altigenis*; posterior base of p4 only slightly broadened, and posterior accessory cusp labially (not centrally) placed; small m3 present; thick, robust dentary below molars. Lacks an enamel swelling at base of m1 posterolingual to protoconid (present in *Delotrochanter petersoni*, a carnivore of about the same size).

DESCRIPTION: The fragmentary mandible of LACM 15908 is about the same depth (28 mm) below the m1 as Cope's type of *Temnocyon altigenis* (29 mm), however, the jaw is thicker and the teeth are larger and more robust (mandibular depth below m2 is similar, ~31 mm in both species). *Delotrochanter petersoni*, smallest species of its genus, has a depth below m1 of ~33 mm; although of about the same size as LACM 15908, its m1 lacks the metaconid and differs in the form of the principal cusps and cingulum. Only the posterior part of p4 is preserved in LACM 15908, anchored in the jaw by the posterior root. This tooth has both a basal cusp and a labially placed posterior accessory cusp. The posterior border of p4 fits tightly against the base of the m1 paraconid. The posterior part of p4 is only somewhat widened, and could be transitional between the plesiomorphic laterally compressed p4 of *T. altigenis* and the posteriorly broad p4 of *M. obtusidens*.

The m1 is a small, well-worn carnassial. The placement of the three trigonid cusps is similar to their position in AMNH 6855, Cope's holotype of *T. altigenis*, however the metaconid is more reduced in LACM 15908. The cusps are more worn than in AMNH 6855, and apical wear is pronounced on all m1 cusps but not present on m2. The broadened talonid of m1 bears a large, rounded hypoconid, nearly centrally situated; lingual to the hypoconid the enamel surface slopes downward to a narrow shelf lacking an entoconid. The labial m1 cingulum is sinuous, not straight as in *D. petersoni*.

The m2 is not elongated as in *M. obtusidens–M. ferocior*. The centrally placed, low, blunt protoconid is the largest cusp; a vestigial paraconid is indicated only by the slightly elevated anterolingual corner of the tooth; there is no metaconid. The hypoconid is lower than the protoconid, is placed directly behind it, and is the sole talonid cusp. The m2 paraconid is not as pronounced as in *M. obtusidens–M. ferocior*, hence LACM 15908 lacks the anteriorly extended m2 trigonid of the latter two species, formed by the paraconid and a protrusion of the anterolabial corner of the tooth. However, the m2 of LACM 15908 could structurally precede the more elongate m2 of *M. obtusidens*. A single alveolus for m3 is present.

The masseteric fossa terminates anteriorly under the posterior part of m2, and the forward inclination of m2–3 on the edge of the ascending ramus of the mandible is evident in LACM 15908 exactly as in *Mammacyon obtusidens*.

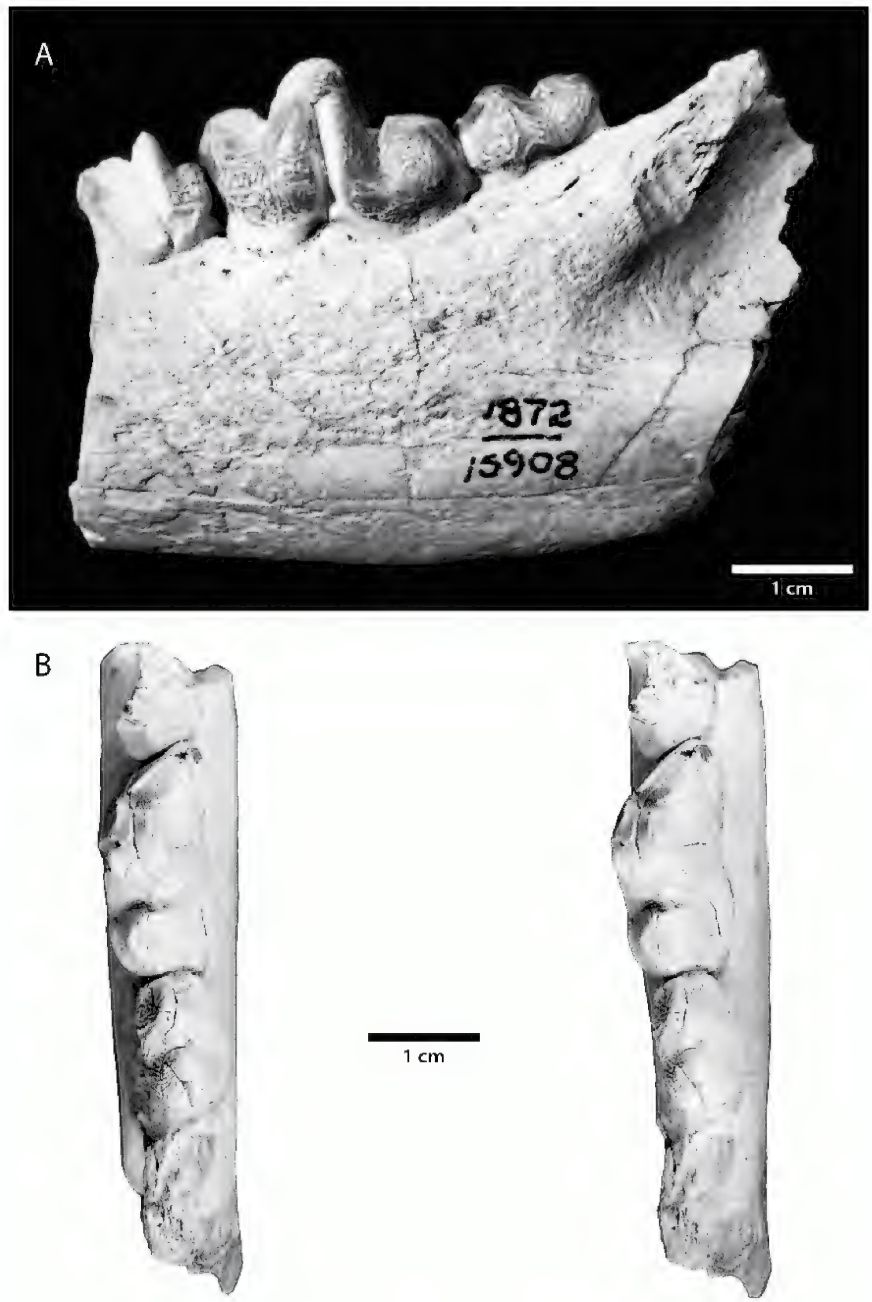


Fig. 32. Tentatively referred mandibular fragment of *Mammacyon* (LACM 15908) with left m1–2 and partial p4, LACM loc. 1872, Sharps Formation, Shannon Co., South Dakota. **A,** labial view; **B,** occlusal stereopair. Note apical wear on m1 cusps.

DISCUSSION: This mandibular fragment, originally identified as a canid, is the earliest evidence of the Temnocyoninae described from the Cenozoic of the North American midcontinent. LACM Locality 1872 occurs in the Sharps Formation with an estimated age of between 28.8 and 29.4 Ma (Tedford et al., 1996, 2004; Macdonald, 1970). The mandible represents a temnocyonine more specialized in its dentition than fossils of

Temnocyon altigenis from the John Day beds of Oregon. *T. altigenis* (UCMP 9999) from Logan Butte is certainly older than ~28.9 Ma, the date obtained on an ash bed near the top of the John Day Formation at the butte, and more likely falls near 29.2–29.3 Ma if collected near dated tuffs at the base of Logan Butte. UCMP 9999 and LACM 15908 could be approximately contemporaneous species, although a somewhat younger age for LACM 15908 seems more probable.

The teeth of LACM 15908, despite small size, have a robust quality much like the larger durophagous temnocyonines of the later Arikareean. The absence of its anterior premolars makes referral to a genus difficult because the short, wide premolars of *Delotrochanter* are diagnostic relative to more plesiomorphic premolars of *Mammacyon* and *Temnocyon*. Lack of the elongate m2 that distinguishes the *Mammacyon* lineage prevents certain referral to that genus but the shorter m2 of LACM 15908 could represent the ancestral state. The labial m1 cingulum appears to be slightly sinuous, a trait present in *Mammacyon*, differing from the straight labial cingulum of *Delotrochanter*. Referral of LACM 15908 to *Temnocyon altigenis* is not appropriate because of the strong reduction of the m1 metaconid and the deep mandible and broader teeth, indicating a more derived carnivore. More complete material of the Sharps temnocyonine will be necessary to establish its identity.

Delotrochanter, new genus

TYPE SPECIES: *Delotrochanter oryktes*, new species.

INCLUDED SPECIES: *Delotrochanter petersoni*, new species; *D. oryktes*, new species; *D. major*, new species.

DISTRIBUTION: Mid- and late Arikareean of northwest Nebraska; latest Arikareean of Nebraska-Wyoming boundary in vicinity of the Niobrara River.

ETYMOLOGY: From the Greek, *delos*, for "evident," and *trochanter*, "runner," to emphasize the cursorial nature of these carnivores.

DIAGNOSIS: Distinguished from *Temnocyon* by absence of the m1 metaconid; by a centrally placed m2 protoconid and hypoconid; and by proportions of P4 and M1 (table 6, ratios A/B, C/D); from *Mammacyon* by a short, less elongate skull, by shorter broad p2–3 and less elongate m2 (ratio E/F); and from *Rudiocyon* by a more elongate m2 (ratio E/F). See tables 1–5.

DISCUSSION: The genus includes temnocyonines that abandon the plesiomorphic form of the cheek teeth and adopt a crushing durophagous dentition different from that of *Mammacyon* in proportions of the carnassial-molar battery. *Delotrochanter petersoni* appears to be a mid-sized ancestral species evolving to the large *D. oryktes* and the even larger *D. major*. The genus ranges in time from the mid- to latest Arikareean but is not certainly known in the early Arikareean interval.

Delotrochanter petersoni, new species
Figure 33

Family Canidae, gen. et sp. indet: Peterson, 1907: 33–34, fig. 6. (The year of publication usually cited for this paper is 1906; however, a printed erratum in a copy in the American Museum's Osborn Library establishes March 21, 1907, as the publication date.)

TYPE: CM 1603, associated lower jaws, with only the left canine, p1, and m1 preserved. Also included under the same catalog number are the M1 protocone, the anterolabial corner of left P4, a metastylar fragment of right P4, a premolar, and four canine fragments. The Carnegie Museum field label records the holotype from the "middle Monroe Creek beds," head of Warbonnet Creek, Sioux County, Nebraska, collected by O.A. Peterson and party, May 1904, but was reported in Peterson's publication (1907: 24) as "from the upper Monroe Creek horizon."

DISTRIBUTION: ?Mid-Arikareean, Arikaree Group, near head of Warbonnet Creek, Sioux County, Nebraska.

ETYMOLOGY: The species name recognizes the paleontologist Olaf Peterson who collected the holotype in northwest Nebraska in 1904.

DIAGNOSIS: Smallest recognized species of *Delotrochanter* with m1 length of 22.3 mm; differs in size from the much larger *D. oryktes* and *D. major*. Distinguished from *Temnocyon* and *Mammacyon* by nearly straight (not sinuous) labial cingulum on m1 and by short,

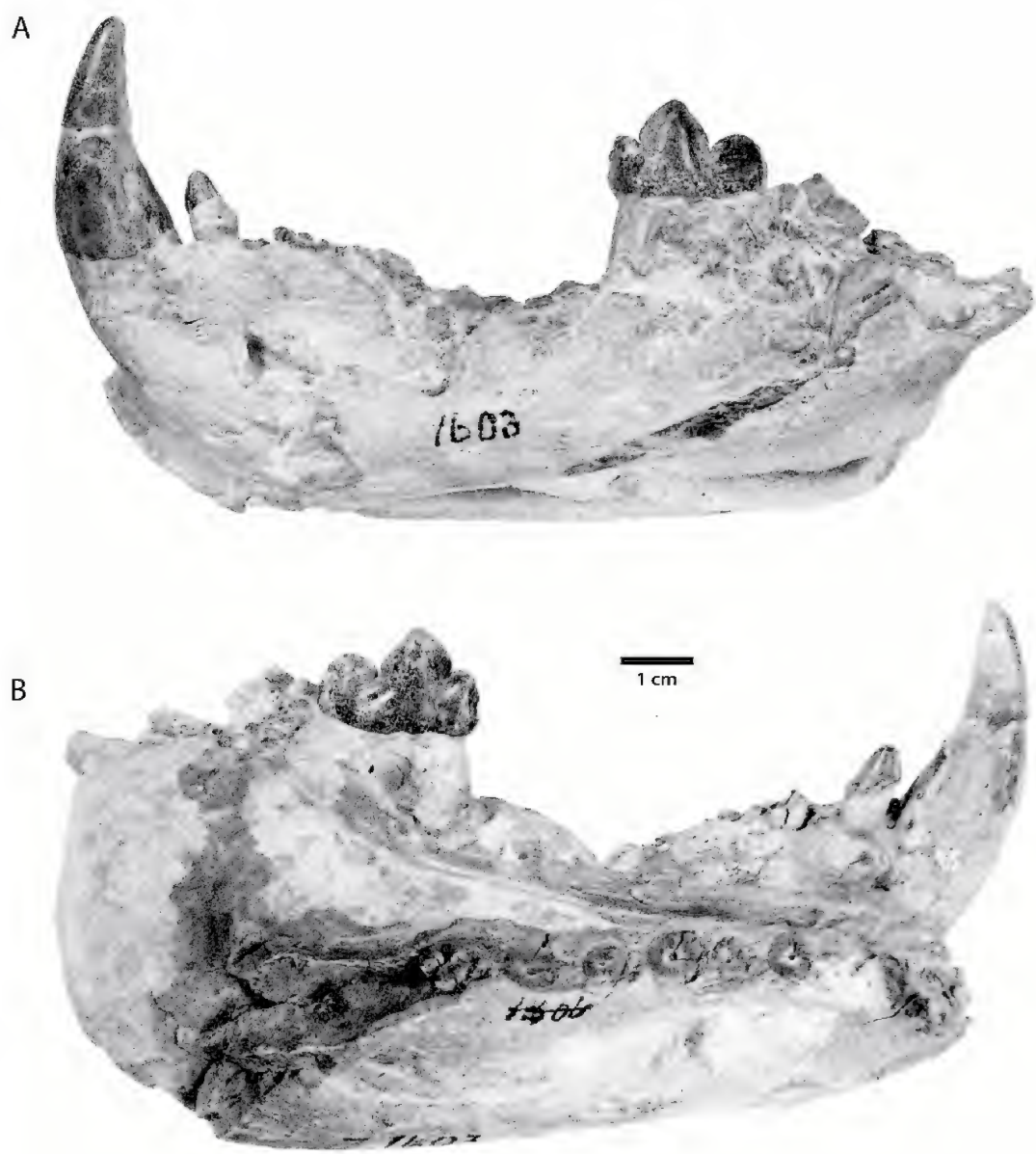


Fig. 33. Holotype mandibles of *Delotrochanter petersoni* (CM 1603), with left canine, p1 and m1, and alveoli for p2–p4, from the Monroe Creek beds (fide Peterson, 1907), head of Warbonnet Creek, Sioux Co., Nebraska. **A,** labial view and **B,** high oblique lingual view of left mandible and the alveoli of right mandible. The m1 lacks a metaconid.

posteriorly broad p2–3. Differs from *Temnocyon* by absence of m1 metaconid; by its m1 paraconid-protoconid-hypoconid triad low, blunt, not specialized for shear and in direct anteroposterior alignment; and from *Rudiocyon* by much smaller size.

REFERRED SPECIMENS: None.

DESCRIPTION: The canine measures 33.3 mm in height from tip to enamel base on the labial face, 12.0 mm in width, and 16.0 mm in length at the enamel base. A wear groove is developed on the

posterolabial surface by the action of the upper canine.

The p1 measures 7.7 mm in length, 5.6 mm in width. It is a simple, conical tooth with an anteriorly placed main cusp and no accessory cusps.

Only roots of p2–4 are present, however they demonstrate that the premolars were closely spaced but not crowded. Labial placement of the anterior root of p2 suggests that the front of the tooth was rotated slightly outward. An important dental trait of *Delotrochanter petersoni* is that p2–3 are short with small-diameter anterior roots, a specialization of the anterior premolars also found in *Delotrochanter oryktes* and *D. major*, thus a defining characteristic of the genus. In *Mammacyon* and *Temnocyon*, p2–3 are elongate teeth with anterior roots of larger diameter.

The m1 measures 22.2 mm in length, 11.3 mm in greatest width (at protoconid), and 10 mm in transverse width across the hypoconid. There is no metaconid; the paraconid is short and robust, much lower than the protoconid, with a paraconid blade 3.7 mm in length. The wide, robust protoconid is 10.1 mm in length measured between the incisures it forms with the paraconid and hypoconid. Its talonid is dominated by a massive, blunt, centrally placed hypoconid that functions as a crushing cusp when applied to the protocone basin of M1. From the hypoconid-protoconid incisure to the rear of the talonid is 7.6 mm. An indistinct cingulum surrounds the base of m1, but this cingulum on the labial side is nearly straight, not sinuous, and is a key feature linking *D. petersoni* to *D. oryktes*.

The m2 was not preserved and its size cannot be accurately determined since both mandibles have been damaged in this area. Peterson (1907: 34, fig. 6) in his description of the specimen stated that "judging from the specimen, m2 was of considerable size." Peterson figured two alveoli for the roots of m2: the anterior alveolus is represented by a root, and the posterior alveolus by a circular depression where a root tip once existed. Estimating the length of m2 from these two alveolar remnants gives an m2 length of ~13 mm, and an m1/m2 ratio of ~1.7, similar to that of *D. oryktes* (ratio E/F, 1.69, table 6).

Little can be said concerning the four isolated canine fragments that accompany CM 1603. However, these fragments and the intact canine in the mandible show that the canines are large teeth relative to the dimensions of the mandible.

The fragment of the anterolabial corner of the left P4 indicates that the upper carnassial had a slightly swollen basal cingulum, and that a fine enamel ridge ran from the tip of the paracone to a point just medial to the anterolabial corner, a typical feature of temnocyonines. In addition, the paracone was a low, blunt cusp as are the m1 cusps. This tooth fragment is configured as in *Delotrochanter* where the anterolabial corner is not anteriorly extended as it is in large *Mammacyon*. A fragment of the metastylar blade of the right P4 shows that the blade was short and broad, measuring 9 mm in length, about 8.2 mm in width. It compares well with the metastylar blade of *D. oryktes* (ACM 4804). An indistinct cingulum surrounds the blade. The fragment is similar in size to the fragmentary P4 metastylar blade of *T. ferox* (YPM-PU 10787) but is more robust. In fact, the narrow blade of *T. ferox* represents a more sectorial carnassial.

A fragment of the left M1 protocone shows that the protocone region was already anteroposteriorly widened. The protocone fragment measures 12.5 mm in anteroposterior width but in life the tooth was wider since the posterior part of the thickened lingual cingulum is missing. The M1 protocone of CM 1603 was knoblike and isolated in an enamel flat surrounded by an expanded lingual cingulum.

The depth of the mandible below m1 is 32.8 mm and below p2 is estimated at 30 mm. This is a rather shallow jaw relative to its thickness (12.9 mm below m1).

Note that Peterson's figure (1907: fig. 6) gives CM 1506 for this specimen, whereas his text reads CM 1603: this last is the correct catalog number and is the only number on the specimens. The specimen labels show that the mandibles initially were given CM 1506 and the isolated teeth fragments assigned CM 1505; all this material later was united under CM 1603.

DISCUSSION: This mandible, collected in 1904, was the first record of Temnocyoninae

in the North American midcontinent, and was believed by Peterson (1907) to be a canid (within the broader meaning of that term as used at that time, i.e., canids and amphicyonids). The few intact teeth present in the left mandible (canine, p1, m1) made identification difficult. However, the following traits suggest that this is the earliest North American representative of *Delotrochanter*:

(1) absence of m1 metaconid, straight labial cingulum on m1, and large centrally placed m1 hypoconid filling the talonid; (2) short p2–3, with small-diameter anterior roots and larger-diameter posterior roots; (3) unexpanded anterolabial corner of P4 like that of *D. oryktes*; low, short P4 metastylar blade; (4) slender, shallow horizontal ramus of the mandible.

Fine-grained gray volcaniclastic sandstone adheres to the mandibles, leaving no doubt as to the sediment in which the fossil was found. Along the Pine Ridge escarpment in Sioux County near the head of Warbonnet Creek, this matrix is typical of the Arikaree Group, and indicates gray volcaniclastic sandstone exposures of the middle and upper part of the escarpment. Peterson's confusing attribution to "middle" Monroe Creek (on field labels) and later on, "upper" (in his published article), at least indicates that CM 1603 came from beds stratigraphically between the lower Arikaree fluvial sandstones at the base of the Pine Ridge and the eolian Harrison Formation sandstones forming the upper part of the escarpment, but prevents an exact stratigraphic designation.

The Pine Ridge escarpment immediately east of Warbonnet Creek includes the stratotypes for the Monroe Creek Formation and Harrison Formation of Hatcher (1902a) at Monroe Creek Canyon. Because Peterson did not attribute the fossil to the Harrison Formation, one can be reasonably confident that CM 1603 did not come from that rock unit as understood by Peterson and Hatcher (i.e., the upper ~200 ft of the Pine Ridge Arikaree escarpment). Hatcher in 1902 described the Monroe Creek Formation as "300 feet of very light-colored, fine-grained, not very hard, but firm and massive sandstones." Based on Peterson's published attribution to "upper Monroe Creek," one would predict that CM 1603 came from fine-grained gray tuffaceous sandstones of the Pine Ridge escarpment ~200–400 ft below the terminal paleosol of the Harrison Formation (Hunt, 1985). These sandstones exhibit large-scale eolian cross-strata, in which CM 1603 was possibly found, that constitute much of the middle part of the Pine Ridge stratigraphic section in Sioux County from Monroe Creek west to Warbonnet Creek. Fossil mammals are rarely encountered in these beds.

Previously I attributed the temnocyonine here named *Delotrochanter petersoni* to an early Arikareean chronofauna (Hunt, 1985: 192) but Peterson's (1907: 24) "upper Monroe Creek" allocation, which places CM 1603 in association with the oreodonts *Promerycochoerus* and *Phenacocoelus*, cannot be ruled out and suggests a younger age. It is at least certain *D. petersoni* occurs in a fauna older than that typical of the Harrison Formation of Peterson. This is supported by the size relationship of *D. petersoni* to its presumed descendant, *D. oryktes*. The latter species occurs in the Harrison Formation in the Niobrara River valley at Agate National Monument, and its predecessor, *D. petersoni*, is of the smaller size and dental features one would predict in "middle to upper Monroe Creek" sediments of the Pine Ridge.

Delotrochanter oryktes, new species
Figures 34–39

"The major part of a skeleton of *Daphoenodon superbus* Peterson ....": Loomis, 1910: 298.

TYPE: ACM 4804, partial skull with right I2–3, C, P1–2, P4–M2, and left I2–3, C (partial), P1–2, P4–M1, labial half of M2; right mandible with c, p4–m2; left mandible with c, p2–4, m1–2; and much of the postcranial skeleton, from the Harrison Formation, *Stenomylus* Quarry, Agate Fossil Beds National Monument, Sioux County, Nebraska, collected by F.B. Loomis, 1908.

DISTRIBUTION: Late Arikareean, Harrison Formation and basal Anderson Ranch Formation, Agate Fossil Beds National Monument, Sioux County, Nebraska.

ETYMOLOGY: From the Greek, *oryktes*, for "digger" or "excavator," in allusion to the discovery of one of the individuals of the species in a burrow.

DIAGNOSIS: Distinguished from *D. petersoni* by larger size (*D. petersoni* m1 length,

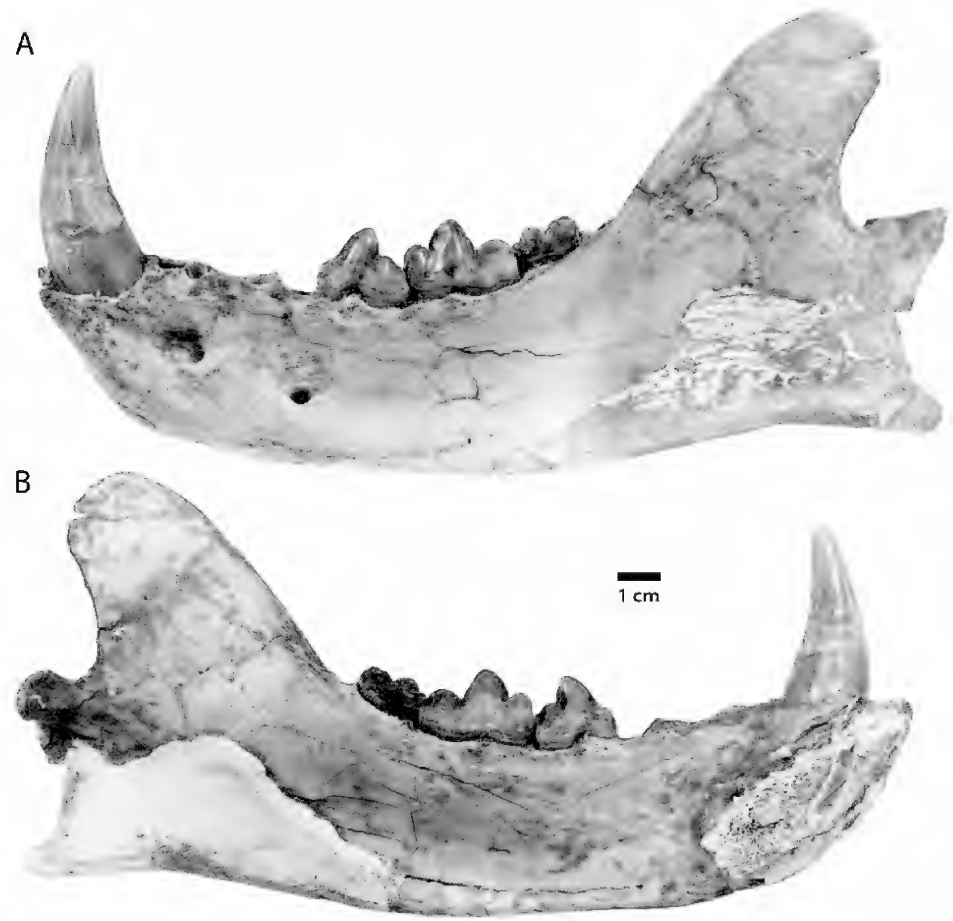


Fig. 34. Holotype mandible of *Delotrochanter oryktes* (ACM 4804) with left canine, p4–m2, alveoli of p1–3, from *Stenomylus* Quarry, Harrison Formation, Agate Fossil Beds National Monument, Sioux Co., Nebraska. **A,** labial and **B,** lingual views. Male individual found with baculum.

22.3 mm; *D. oryktes* m1 length, 27.1 mm). Dentition clearly antecedent to that of the much larger *D. major* (tables 2, 3), but not as massive and robust. Differs from *Temnocyon* by loss of the m1 metaconid and by short, posteriorly wide p2–3 and P2–3; from *Mammacyon* by a posterior accessory cusp on p3, a large centrally placed posterior accessory cusp on p4, and by a smaller P4 with lingually abbreviated protocone region; and from *Rudiocyon* by the form of p4.

REFERRED SPECIMENS: (1) UNSM 47800 (field no. 8-81), partial skull with left P2–M2, lingual half of right M1, right I2–3, and petrosal fragment; associated left calcaneum, left metatarsals 2–4, left metacarpals 3–5 with proximal phalanx and 2 sesamoids, left magnum; found in place within a burrow, Carnegie Quarry 3, Beardog Hill den site, Agate Fossil Beds National Monument, Sioux County, Nebraska, collected September 14, 1981, by J. Kaufman and R.M. Hunt (UNSM field no. 9-81 was given to the fifth metacarpal, found near the skull, presumably from the same individual); (1a) CM 1589b, right metatarsal 5, Carnegie Quarry 3, Beardog Hill den site, collected by O.A. Peterson, 1904–1905, probably the same individual as UNSM 47800; (2) YPM-PU 24872, left calcaneum, removed from Princeton University quarry block (now YPM-PU 12213), Princeton Expedition of 1914, loc. 1002A, Carnegie Hill waterhole bonebed, Agate Fossil Beds National Monument, Sioux County, Nebraska.

Fig. 35. Holotype mandible of *Delotrochanter oryktes* (ACM 4804) with left canine, p2–m2 (p2–3 inserted in mandibular alveoli to demonstrate small diameter of anterior roots).

DESCRIPTION: Both individuals referred to this species (ACM 4804, UNSM 47800) come from Agate Fossil Beds National Monument, Sioux County, Nebraska, and were collected 73 years apart. ACM 4804, designated here as the holotype, includes a nearly complete skeleton discovered by Loomis at *Stenomylus* Quarry in 1908. It was originally referred to *Daphoenodon superbus*: Loomis (1910) did not recognize it as a temnocyonine, a group almost unknown at that time. A second individual (UNSM 47800) is represented by a skull (fig. 37) and bones of the fore- and hind feet, found within a carnivore burrow (front cover) during the reopening of Carnegie Quarry 3 by the University of Nebraska in 1981 (Hunt et al., 1983; Hunt, 1990: 106–107).

The mandible and lower dentition are known in ACM 4804 but were not recovered with UNSM 47800. The following description is based on ACM 4804; it is selected here as the holotype of the species because of the association of maxillary and mandibular dentition with the postcranial skeleton (see Postcranial Osteology). Appropriate comparisons are made with the larger derivative species, *D. major*, known only from teeth.

The mandible is deep yet thin, with a distinctive recurved coronoid process and a wide (35.8 mm) articular condyle. The anterior margin of the ascending ramus curves gradually downward beneath the rear molars so that m2–3 are forwardly inclined as in several other temnocyonines. The nearly uniform depth of the horizontal ramus is demonstrated by similar measurements beneath m1 (45.7 mm) and p2 (41 mm). Length of the mandible measured from the symphysis (between the first incisors) and the posterior surface of the articular condyle is 205 mm.

Lower incisors did not survive in either individual referred to this species. Alveoli for i1–3 are present in the left mandible of ACM 4804: the single alveolus for i3 (width, 4.5 mm) shows that it was the largest of the lower incisors. A smaller i2 alveolus is situated medial to i3, and a very small i1 alveolus is placed slightly internal and ventral to i2.

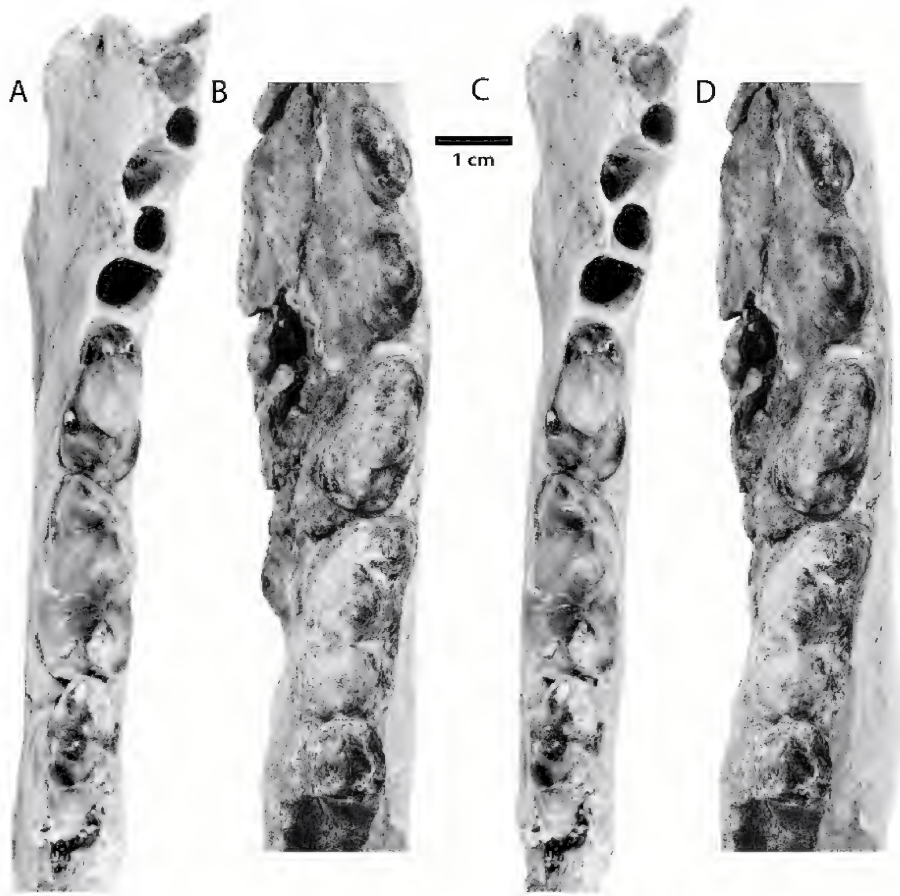


Fig. 36. Occusal stereopairs of the holotype mandibles of (**A, C**) *Delotrochanter oryktes* (ACM 4804) and (**B, D**) *Delotrochanter major* (F:AM 27561). *D. oryktes*, right p4–m2, alveoli of p1–3; *D. major*, left p2–m2. Note absence of m1 metaconids and relative anterior and posterior alveolar diameters of p2 in *D. oryktes*. The p4–m2 are crushing teeth in both species.

The left lower canine of ACM 4804 is not as strongly recurved as in some species of *Temnocyon* (UCMP 9999, YPM-PU 10787). Canine height from the base of the enamel to the unworn tip on the labial side is 36.8 mm. Length and width measured at the base of the enamel are 18.5 mm and 12.5 mm, respectively. A pronounced enamel ridge runs from the tip to the enamel base on the posterior edge, and a second ridge travels down the anterolingual face. Although the m1 of a wolf is about the same size as the *D. oryktes* m1, the beardog canine is much larger.

The p1 is not preserved in ACM 4804; the single large alveolus measures 8.2 mm in length, 6 mm in width, and is crowded between the canine and p2 alveoli, and is in contact with both. Closely spaced alveoli are common to the entire lower toothrow. The slight crowding of premolar alveoli is due to the youth of this carnivore (all teeth are only in early wear).

The p2 is a tall, yet anteroposteriorly short, double-rooted tooth, 14.9 mm in length, 8.2 mm in greatest width. There is no posterior accessory cusp. The anterior face is steeply inclined and is traversed by a fine enamel ridge that extends from tip to anterolingual cingulum. The posterior face is more gradually inclined with an enamel ridge running from tip to posterolabial cingulum. The anterior root of p2 is much smaller (length, 4.9 mm) than the robust posterior root (length, 8.5 mm), a distinguishing trait of the species.

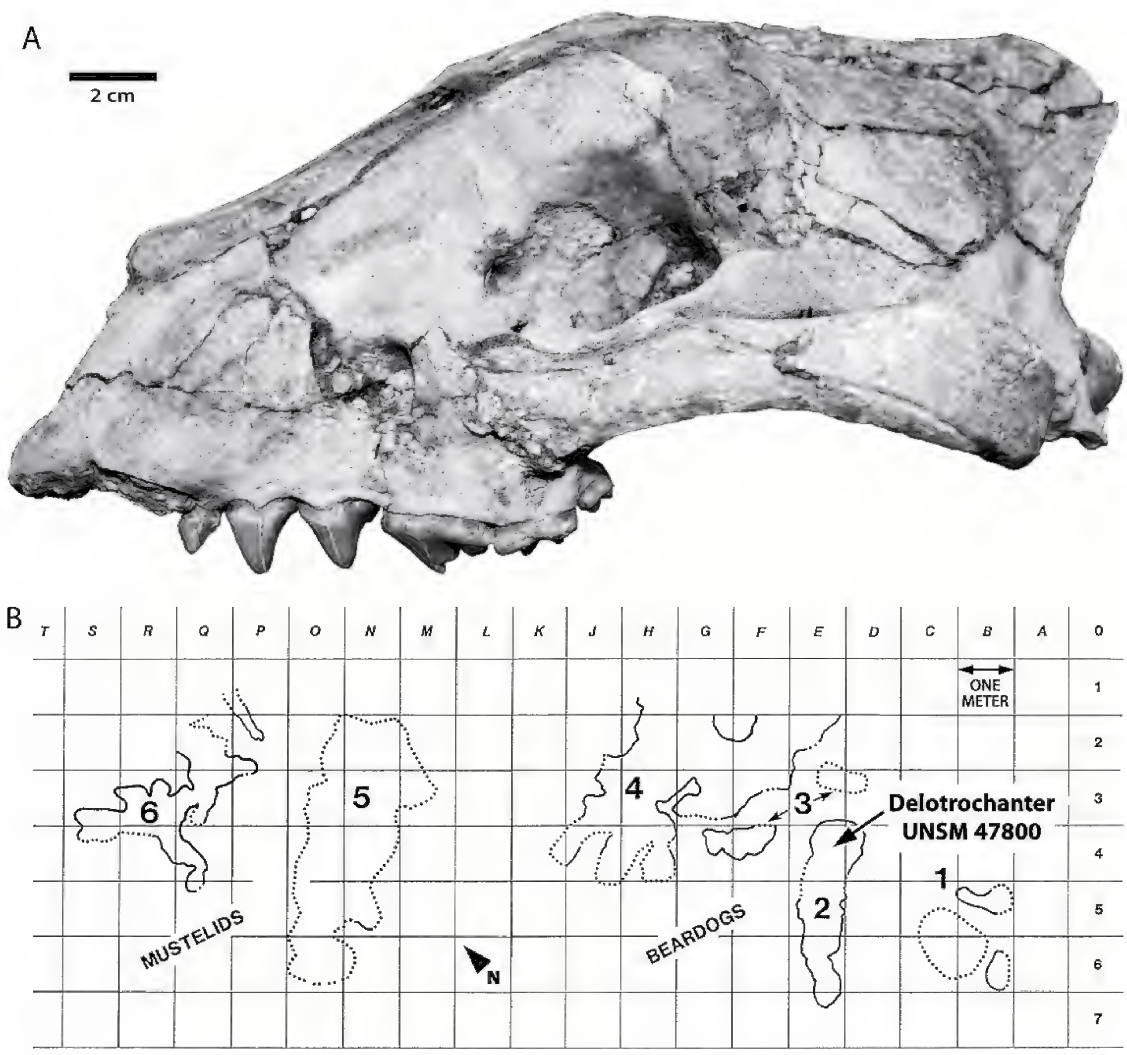


Fig. 37. **A,** *Delotrochanter oryktes* (UNSM 47800), cranium with P1–M2 of presumed female from carnivore den, Beardog Hill, Agate Fossil Beds National Monument, Sioux Co., Nebraska. The short, deep hyenalike skull is unique among temnocyonines. **B,** Plan map of dens showing location of burrow (den 2) that contained the skull and foot bones of *D. oryktes* (UNSM 47800). The beardog *Daphoenodon superbus* was the principal occupant of dens 1, 3, and 4; mustelids were found in dens 5 and 6.

The p3 measures 16.6 mm in length, 9.4 mm in posterior width, and 6.9 mm in anterior width. The tooth is short and posteriorly wide, which is evident when compared with the respective dimensions of p3 in *Mammacyon ferocior* (19.3 mm, 9.0 mm, 6.8 mm). There is a posterior accessory cusp, somewhat labially placed. A slightly swollen basal cingulum is more pronounced on the lingual and posterior sides. Just as for p2, the anterior root is smaller than the posterior root.

The p4 is robust, with a wide heel, measuring 21.0 mm in length, 10.8 mm in posterior width, and is much larger than p3. Its form is diagnostic of the genus, notably the large posterior accessory cusp centrally placed on an expanded heel behind the principal cusp. *Delotrochanter* is the only temnocyonine that has evolved a centrally placed posterior accessory cusp on p4. In *Temnocyon* and *Mammacyon* the accessory cusp is labially placed.

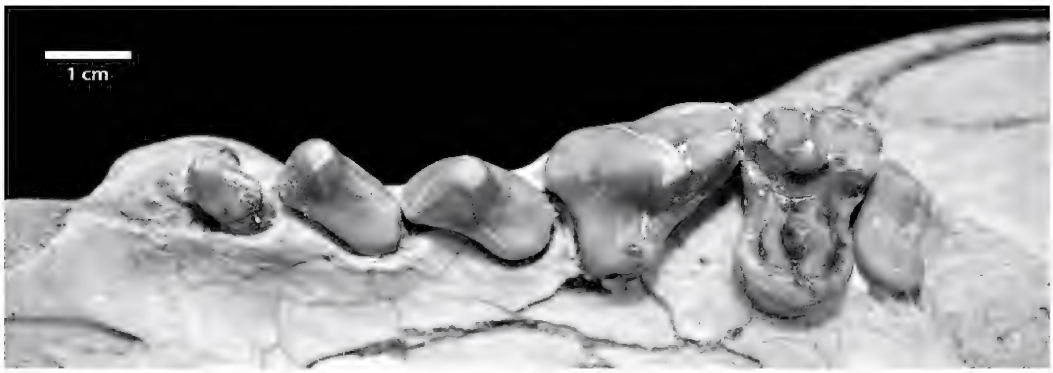


Fig. 38. Left maxilla of the *Delotrochanter oryktes* cranium (UNSM 47800) with P1–M2, presumed female, Beardog Hill, Agate Fossil Beds National Monument, Sioux Co., Nebraska. The crushing P4–M1 is more gracile than these teeth in the male (ACM 4804, fig. 39).

The height of the principal cusps of p2–4 is pronounced, so much so that the linear serial alignment of the premolar cusps is continued along the toothrow by the principal cusps of m1 and m2, and this cusp alignment is further emphasized by the elevation of m2–3 on the rising margin of the ascending ramus.

The m1 is a crushing carnassial, 27.1 mm in length, 12.7 mm in greatest width, formed by three aligned bunodont cusps, the paraconid-protoconid-hypoconid. There is no metaconid or entoconid. The thickened labial cingulum is essentially straight, not sinuous as in *Temnocyon* and *Mammacyon*. The hypoconid is centrally placed on the talonid and in labial view is as tall as the paraconid (as in *Mammacyon* but not *Temnocyon*). The nearly equal development of hypoconid and paraconid flanking the protoconid creates a profile typical of large species of *Mammacyon* and *Delotrochanter*, but a somewhat larger hypoconid in *Delotrochanter* emphasizes the cusp alignment adapted for crushing.

Fig. 39. Right maxilla with P4–M2 of *Delotrochanter oryktes* (ACM 4804, male), *Stenomylus* Quarry, Harrison Formation, Agate Fossil Beds National Monument, Sioux Co., Nebraska.

The m2 is rectangular in occlusal view, measuring 16.0 mm in length, 10.0 mm in greatest width (m1/m2 length ratio, ~1.7, table 6). The protoconid and hypoconid are placed in direct anteroposterior alignment behind the m1 hypoconid. These three cusps are about the same height and form a crushing battery posterior to the carnassial blade. There is a low vestigial paraconid. The m2 is not as elongate (relative to m1 length) as in *Mammacyon*, but the cusps of m2 are centrally placed as in that genus. Hence, one of the hallmarks of *Delotrochanter* is the central placement of all cusps from p4 to m3 (with slight lingual diversion of the m1 paraconid).

The m3 is not preserved but is represented in ACM 4804 by a single large alveolus, length 5.3 mm, width 5 mm.

In ACM 4804, p1–m3 length is 104.5 mm; p2–m2 length, 89.6 mm; p1–4 length, 59.7 mm; m1–3 length, 48.2 mm.

The skull of ACM 4804 was damaged during preparation and mounting of the specimen at Amherst College shortly after it was collected in 1908. With the aid of Drs. Margery and Walter Coombs, we were able to recover the skull and restore part of the

rostrum and palate and a few basicranial fragments, including the right petrosal and a partial basioccipital.

The central incisors (I1–2) of ACM 4804 are much smaller than I3. I1 is not preserved in ACM 4804, however the alveolus measures 9.3 mm in length, 4.1 mm in width. I2 is present with a vertical anterior face, a sloping posterior surface, and a prominent auxiliary cusp (Nebenzacke) on its lateral margin. I2 is 9.8 mm in length, 5.7 mm in width at the enamel base. I3 is a large, recurved caniniform tooth measuring 23.2 mm in height from tip to posterolabial enamel border, 13.1 mm in length, 10.1 mm in width at the base of the enamel. I3 has a thin enamel ridge from tip to posterolabial base and another on the lingual face from tip to enamel base. I2–3 in UNSM 47800 show no differences from those incisors in ACM 4804.

The upper canine measures 37.9 mm in height from its posterolabial enamel base to its unworn tip. Length and width at the base of the enamel are 19.3 and 13.4 mm. An enamel ridge runs from the tip to the enamel base on the posterior surface; a second ridge runs from tip to base on the anterolingual surface.

P1 is a small, conical tooth 9.4 mm in length, 6.9 mm in greatest width. There is a single principal cusp and no accessory cusp. The principal cusp is placed forward of center, and from this cusp a fine enamel ridge extends down both the anterior and posterior faces of the tooth.

P2 is much larger than P1, measuring 15.8 mm in length, 8.7 mm in posterior width (in UNSM 47800, P2 measures 15.9 mm and 8.0 mm). P2 is tall, triangular in lateral view, with a vertical, nearly rectilinear anterior face and a more gradually sloping posterior face. Of importance is the small anterior root relative to the larger posterior root, a diagnostic feature of *Delotrochanter*, indicating that the shortening of p2 in the lower jaw is reciprocated in the upper dentition. Alveolar length of the P2 anterior root is 5.6 mm; posterior root, 10.0 mm; length of the roots themselves are, respectively, 5.2 and 8.8 mm. The posterior heel of P2 is widened and a weak accessory cusp is labially placed low on the broad heel. Thin enamel ridges are present on the anterior and posterior faces of P2, running to the respective anterolingual and posterolabial corners.

P3 is lost from the skull of ACM 4804 but is present in UNSM 47800 (length, 18.2 mm; width, 9.8 mm) where it is about the same height as P2 but posteriorly wider with a small accessory cusp slightly labially situated on the posterior slope.

P4 measures 21.4 mm in labial length, 18.8 mm in greatest transverse width across the protocone. This massive tooth has a short metastylar blade 9 mm in length that forms a moderately developed shear surface with the large paracone. Small vertical wear facets are developed on the lingual faces of metastylar blade and paracone but the predominant crushing mode of occlusion is evidenced in this young individual by blunt-cusp wear on the paracone. As in the larger temnocyonines, the rounded blunt protocone is enlarged for crushing but is not as massive as in species of *Mammacyon*. The protocone in *Delotrochanter* does not extend as far toward the midline of the palate as it does in *Mammacyon*, and does not reach the lingual margin of M1. P4 length is 22.8 mm and width is 17.9 mm in UNSM 47800, too young an individual to develop shear facets on P4.

M1 measures 17.7 mm in length of the labial margin, 25.4 mm in greatest transverse width, and 14.7 mm in anteroposterior width of the protocone region. In UNSM 47800, M1 length is 17.5 mm; greatest width is 23.9 mm; and width across the protocone is 14.1 mm, thus a smaller molar relative to the M1 in ACM 4804. An M1 that is constricted at the level of the protocone basin so that the tooth has a "waist" is typical of *Delotrochanter* and *Mammacyon*. The labial half of M1 is formed by a prominent, yet rather blunt, paracone and somewhat smaller metacone bordered by a labial cingulum thickened in the parastylar region. The lingual faces of the paracone and metacone form a vertical shear surface but these cusps are lower and shear is not as developed as in large species of *Temnocyon*. The low protocone is isolated within an enamel platform, creating a flat crushing surface surrounded by a much-thickened lingual cingulum. A preprotocrista runs from the protocone to the anterior

cingulum at the base of the paracone but there is no postprotocrista. On the M1s of both ACM 4804 and UNSM 47800 the lingual cingulum thins abruptly at the level of the protocone basin. The lingual cingulum of UNSM 47800 is not as developed as in ACM 4804.

M2 is a rectangular tooth, much smaller than M1, measuring 9.3 mm in labial length, 17.4 mm in greatest width (M2 length, 8.9 mm; width, 15.3 mm in UNSM 47800). The paracone is much larger than the strongly reduced metacone, both bordered by a labial cingulum thickened in the parastylar region. The lingual faces of para- and metacone form a low shear surface that continues the paracone- metacone shear plane of M1 (this plane less evident in UNSM 47800 in which M2 is more reduced). The M2 protocone is a low, blunt cusp isolated on an enamel platform surrounded by a slightly thickened lingual cingulum. There is no evidence of M3 although that part of the maxilla where M3 would occur is not preserved. However, UNSM 47800 has an intact maxilla in which M3 is certainly absent.

The skull (UNSM 47800) found in 1981 within a burrow at Beardog Hill, Agate Fossil Beds National Monument preserves the left P1–M2 (figs. 37–38). This is the only known skull of *Delotrochanter*. The left side of the skull and upper dentition are largely intact, whereas the right side was destroyed by plant roots that invaded the burrow. The skull is remarkably similar in form to the skull of the hyena, *Crocuta crocuta*. Both skulls are broad and rather short with laterally extended zygomatic arches and large temporal fossae indicating well-developed temporal jaw musculature. Both have blunt, short snouts of similar length: the preorbital proportion of skull length in UNSM 47800 is 40% and in the hyena 35%. UNSM 47800 differs from *Crocuta* in possessing a more inflated frontal region and more massive snout with larger canines. The infraorbital foramen of UNSM 47800 is much larger than this foramen in the hyena, suggesting a more developed neurovascular supply to the nasal region. The braincase of UNSM 47800, despite the rather short skull, is the largest of any known temnocyonine (table 7).

The upper teeth are extremely similar in form to those of ACM 4804 but are somewhat smaller and more gracile. P4 is longer and its protocone not as developed, and the M1–2 are smaller, not as hypertrophied as in ACM 4804. The crushing function of P4–M2 is better developed in ACM 4804. ACM 4804 is a male (a baculum was found with the skeleton) and, based on the gracile teeth, UNSM 47800 could be a female. Sexual dimorphism is common among amphicyonids and it would not be surprising to find it present in temnocyonines. Dimorphism in temnocyonine species is difficult to demonstrate because of the lack of multiple individuals from a single locality.

DISCUSSION: *Delotrochanter* is defined on the basis of the holotype dentition and skeleton of *D. oryktes* (ACM 4804) supplemented by information derived from the individual (UNSM 47800) found in the carnivore dens at Agate National Monument. These two individuals are clearly closely related and are assigned here to a single species, diagnosed by short, posteriorly wide premolars (p2–4, P2–3) with centrally (not labially) placed posterior accessory cusp on p4. These premolars differ from the longer premolars and labially placed p4 posterior accessory cusp found in *Temnocyon* and *Mammacyon*. Although the p4 of *Mammacyon ferocior* is broader than that of *M. obtusidens*, the posterior accessory cusp in both species remains labial in position. Also, *Delotrochanter oryktes* does not have as prominent a protocone on P4 as in *Mammacyon* nor is its m2 as elongate; and it lacks the m1 metaconid found in *Temnocyon*. These differences, however, are most readily observed in relatively complete dentitions: isolated teeth will in many instances be difficult to assign.

The mandible of ACM 4804 is only ~2 cm longer than that of a mature female Alaskan wolf (ZM 17459: mandibular length, 18.5 cm; basilar length, 22 cm); yet mandibular depth and the height of the coronoid process are much greater and the canine, premolars, and m2 are conspicuously larger and more robust. The m1 is about the same length, but is a wider, blunt-cusped tooth, its protoconid-paraconid lacking the sharp edges seen on the m1 shearing blade of the wolf.

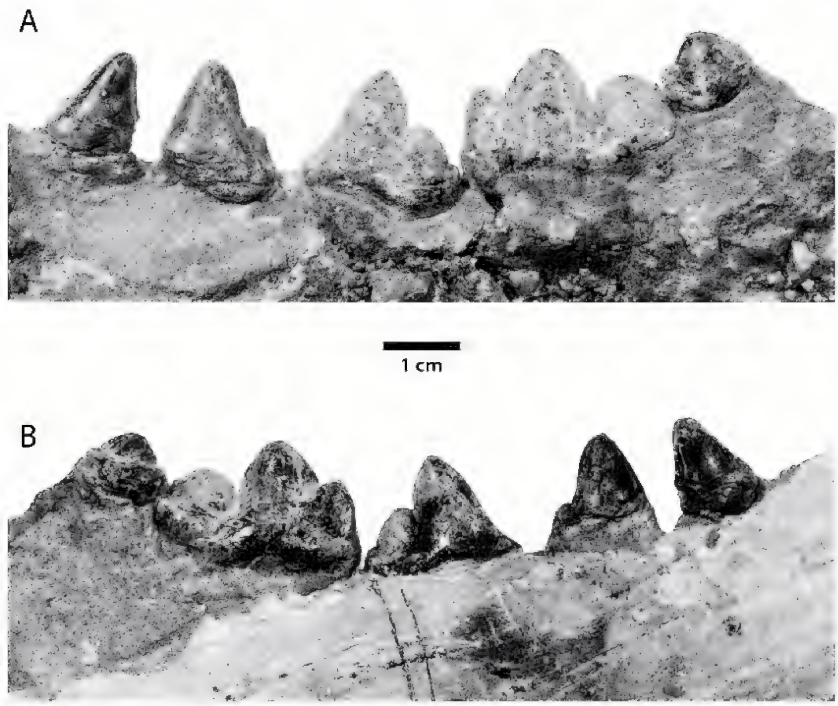


Fig. 40. Holotype dentition of *Delotrochanter major* (F:AM 27561), left p2–m2 (p2, p3, and m2 damaged), Anderson Ranch Formation, near Van Tassell, Niobrara Co., Wyoming. **A,** labial and **B,** lingual views.

The feeding strategy of *D. oryktes* relied on powerful jaw musculature applied to a deep, rigid mandibular "beam" carrying the heavy, blunt premolar and molar crushing dentition with enormous canines.

The four individuals of *D. oryktes* from Agate National Monument occur at three superposed stratigraphic levels: (1) ACM 4804, the holotype, was found ~12–15 m above the two principal camel-producing horizons at *Stenomylus* Quarry in the Harrison Formation (a second individual, ACM 4804A, a juvenile, was found with ACM 4804 but is known only from postcranials); (2) The calcaneum (YPM-PU 24872) indicates the presence of *D. oryktes* in the Agate waterhole bonebed (basal Anderson Ranch Fm.), which occurs stratigraphically between the levels of ACM 4804 and UNSM 48700; (3) The adult (UNSM 47800) discovered in the carnivore dens at Beardog Hill (Hunt et al., 1983: fig. 1, den 2, burrow C) also occurs in the basal Anderson Ranch beds (the dens are excavated into the waterhole bonebed). The amount of time intervening between these stratigraphic levels remains uncertain. The age of ACM 4804 is approximated by the Agate Ash, recently redated at ~22.9 Ma (Izett and Obradovich, 2001).

Despite its younger stratigraphic age, UNSM 47800 is the smaller, more gracile animal relative to ACM 4804. Given the baculum found with ACM 4804, the size difference between UNSM 47800 and ACM 4804 is more likely due to sexual dimorphism and not relative stratigraphic position.

The postcranial skeleton of ACM 4804 is discussed under Postcranial Osetology.

Delotrochanter major, new species
Figures 36, 40–42

TYPE: F:AM 27561, right and left lower canines; partial p2–3, complete p4–m1, m2 trigonid, all of the left side; right p3–m1; an upper canine, right P2–4, maxilla fragment with right I1–3, left I1–2, and right P1 in matrix, from the Anderson Ranch Formation, collected by Paul Miller in 1927 from

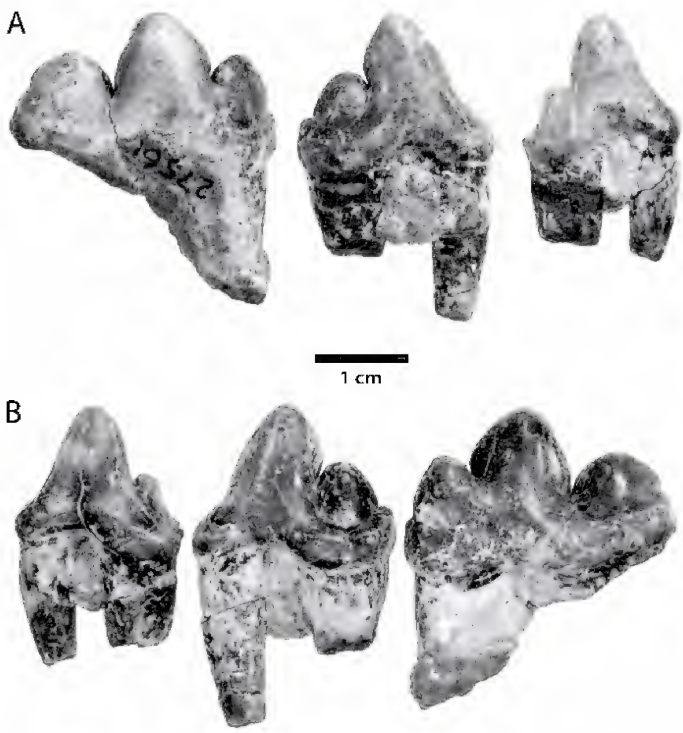


Fig. 41. Holotype dentition of *Delotrochanter major* (F:AM 27561), right p3–m1, Anderson Ranch Formation, near Van Tassell, Niobrara Co., Wyoming. **A,** labial and **B,** lingual views. Note large p4 relative to the carnassial in this terminal species of *Delotrochanter*.

the vicinity of Van Tassell, Niobrara County, Wyoming.

DISTRIBUTION: Latest Arikareean, Anderson Ranch Formation, near Van Tassell, Niobrara County, Wyoming.

ETYMOLOGY: From the Latin, *major*, "greater," in reference to the large size of the terminal species of this genus.

DIAGNOSIS: Distinguished from *D. petersoni* by larger size (m1 length: *D. petersoni*, 22.3 mm; *D. major*, 28.0 mm). All *D. major* teeth are larger and more robust than the equivalent teeth of its predecessor *D. oryktes* (tables 2, 3). Differs from *Temnocyon* by loss of the m1 metaconid and by short, posteriorly wide p2–3 and P2–3; from *Mammacyon* by a posterior accessory cusp on p3, a large centrally placed posterior accessory cusp on p4, and by a smaller P4 with lingually abbreviated protocone region; from *Rudiocyon* by the form of p4.

REFERRED SPECIMENS: None.

DESCRIPTION: Neither mandible of *D. major* (F:AM 27561) survived. The dentition is embedded in series in sediment without mandibular bone supporting the teeth. Thus only *D. oryktes* (ACM 4804) and *D. petersoni* demonstrate the form of the mandible in *Delotrochanter*.

In F:AM 27561, the left lower canine measures 36.6 mm in height from the slightly worn apex to the labial enamel-dentine junction (estimated unworn height, ~40 mm); length and width at the base of the enamel are respectively 18.4 mm and 12.8 mm. The posterolabial surface is grooved by the upper canine; a second wear facet made by I3 occurs at the base of the anterolingual face. In other respects the tooth is similar to ACM 4804.

The p1 is not preserved, and only the main cusp of the left p2 remains; this indicates a tall principal cusp—there are no evident differences from p2 of ACM 4804.

The p3 measures 17.7 mm in length, 10.2 mm in greatest width, and is nearly identical to ACM 4804 except in its larger size and greater posterior width. A centrally placed posterior accessory cusp is present.

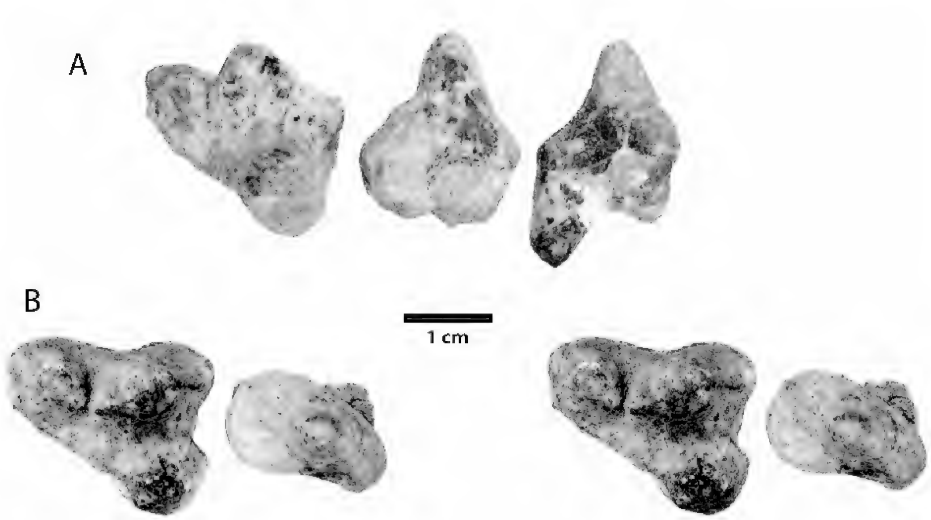


Fig. 42. Holotype maxillary teeth of *Delotrochanter major* (F:AM 27561). **A,** lingual view of right P2–4. **B,** stereopair of right P3–4; enamel was etched by plant roots.

The p4 measures 21.6 mm in length, 9.2 mm in anterior width, 12.3 mm in posterior width; its posterior accessory cusp is very large, centrally placed, and surrounded by a well-defined cingulum, which becomes less conspicuous anteriorly on both lingual and labial sides. The heel of p4 is much wider than in ACM 4804 as is true for p3.

The m1 is similar in all respects to that of ACM 4804 but is more massive and robust, measuring 28.0 mm in length, 14.1 mm in greatest width. Although these lower carnassials were undoubtedly capable of limited shear (vertical wear facets occur on the paraconid-protoconid blade), the premolars, m2–3, and m1 functioned primarily as crushing instruments. The m1 hypoconid and the protoconid of m2 are blunt, low cusps, and in this species could have served no role other than crushing.

The m2 is represented only by the trigonid. It is similar to the m2 trigonid of *D. oryktes* but is more massive, having a very large, blunt protoconid and small vestigial paraconid with a strong labial cingulum; there is no metaconid. Trigonid width is 10.6 mm. Based on similarity of the cheek teeth in F:AM 27561 and ACM 4804, the complete m2 of *D. major* was a larger version of the m2 in *D. oryktes*.

The m3 was not preserved but would have been present.

I1–I2 are of equal size and similar cusp form. Both have a vertical anterior face and a curvilinear posterior surface, and both possess prominent auxiliary cusps (Nebenzacken) on their lateral margins as in *D. oryktes*. I2 measures 9.9 mm in length, 5.6 mm in width; I1 measures 9.1 mm in length, 5 mm in width. The large I3 measures 22.8 mm in height, 13.3 mm in length, and about 10 mm in width at the enamel base. There is a wear groove on the posterolabial face of I3 made by the upper canine.

P1 has the same subconical form as in ACM 4804 and measures 9.4 mm in length by 6.9 mm in width.

P2 is much larger than P1; it is tall, subtriangular in labial view, with near-vertical anterior and more inclined posterior faces, and measures 17.0 by 9.0 mm. The heel of P2 is broad; the thin enamel ridge on the posterior slope ends in a minute cingular cuspule at the posterolingual corner.

P3 is tall, triangular in lateral view, and posteriorly broad, measuring 18.7 mm in length, 11.9 mm in posterior width. The posterior face has a small, labially situated, posterior accessory cusp. P3 has fine enamel ridges on its anterior and posterior faces; the anterior ridge terminates at the anterolingual margin of these teeth; the posterior ridge at the posterolabial corner. The expansion of the heel of both P2 and P3 is more pronounced than in *D. oryktes*.

P4 measures 23.5 mm in length, 19.8 mm in width across the protocone, and is similar

in form to the P4 of ACM 4804 but is larger and slightly more robust. The metastylar blade is blunt as is the protocone; both are essentially unworn, and the slightly worn paracone shows only a flat apical wear facet. Vertical shear, although possible, appears to have been secondary to a crushing action.

The upper molars of *D. major* were not recovered, but based on the remaining teeth they would be similar in form yet somewhat larger than M1–2 of *D. oryktes*.

DISCUSSION: F:AM 27561 differs from *D. oryktes* in larger size and in the greater accentuation of many defining features of the cheek teeth. Not only are its teeth larger but cingula are more pronounced, the cusps more massive, and p3–4 and P2–3 are posteriorly broadened. The defining dental traits of *Delotrochanter* are evident and indicate that *D. major* is clearly derived from *D. oryktes*. Paul Miller, the collector, reported that F:AM 27561 came from the "vicinity of Van Tassell," Wyoming. Near the town of Van Tassell only the Harrison Formation and the Anderson Ranch beds outcrop in the area where Miller worked. Fortunately, sediment adhering to F:AM 27561 shows the pale reddish-brown patina of the Anderson Ranch sandstones. The advanced features of its dentition indicate that Miller may have obtained F:AM 27561 stratigraphically high in the Anderson Ranch beds in the stratotype area of the formation in the Niobrara Canyon (see Hunt, 2002b: 35–39), which is in proximity to the town of Van Tassell. F:AM 27561 is of latest Arikareean age and represents the youngest occurrence of *Delotrochanter*. More than 80 years of exploration of Anderson Ranch Formation outcrops in northwest Nebraska and Wyoming have failed to yield additional remains of this rare temnocyonine since Miller's fortunate discovery.

The stratigraphic levels that produced *D. oryktes* are well documented, and the horizon that yielded *D. major* can be reliably estimated. The stage of evolution of these two species of *Delotrochanter*, which occur in late to latest Arikareeean time, can be contrasted with that of *Mammacyon*. The occurrence of the terminal and largest species, *M. ferocior*, preceded the earliest occurrence of *D. oryktes* in the Harrison Formation at *Stenomylus* Quarry. Thus, the *Mammacyon* lineage reached its apex at a time before 23 Ma, when the coeval species of *Delotrochanter* must have been a much smaller carnivore in the same geographic region.

DENTITION AND FEEDING: APPEARANCE OF DUROPHAGOUS AMPHICYONIDS

The teeth of the geologically oldest temnocyonine, *Temnocyon altigenis*, resemble the teeth of the dentally plesiomorphic beardog *Daphoenus vetus*; both are small carnivores of similar size. *T. altigenis* differs, however, in its larger carnassials, taller premolars, smaller m2, and lack of M3. During the mid-Cenozoic, the temnocyonine dentition departed from this plesiomorphic condition. In the wolf-sized *Temnocyon fingeruti*, a hypercarnivorous pattern was retained, and was scaled to formidable size in the largest species of the genus, *T. macrogenys*. Alternatively, a crushing dental battery also arose from the plesiomorphic type, and attained its maximum development in the large species of *Mammacyon* and *Delotrochanter*.

DENTITION: The upper cheek teeth (P3–M2) best show this progressive shift in dental pattern (fig. 43). In *Temnocyon altigenis* (UCMP 9999, fig. 4A) and *T. subferox* (YPM 10065, figs. 10A, 43A) the shearing carnassial retains a bladelike form with the protocone advanced in the anterior direction, leaving a large embrasure between P4 and M1 for the lower carnassial. This is the primitive amphicyonid condition, also common to primitive arctoid and cynoid carnivorans. M1 is essentially a triangular tooth in occlusal view, its lingual half somewhat broader than in *Daphoenus*, and flanked by a small elliptical M2. M3 is lost in all temnocyonines, unlike most daphoenine and amphicyonine beardogs. P3 remains a narrow premolariform tooth.

In younger species of *Temnocyon* a subtle change in the cheek teeth has taken place. In *Temnocyon ferox* (fig. 43B), body size has increased and the form of P4 and M1 has been modified. A shearing carnassial is still present, yet the tooth is wider and the protocone retracted posteriorly and enlarged relative to *T. altigenis* and *T. subferox*. M1 is less triangular, more quadrate in form, and

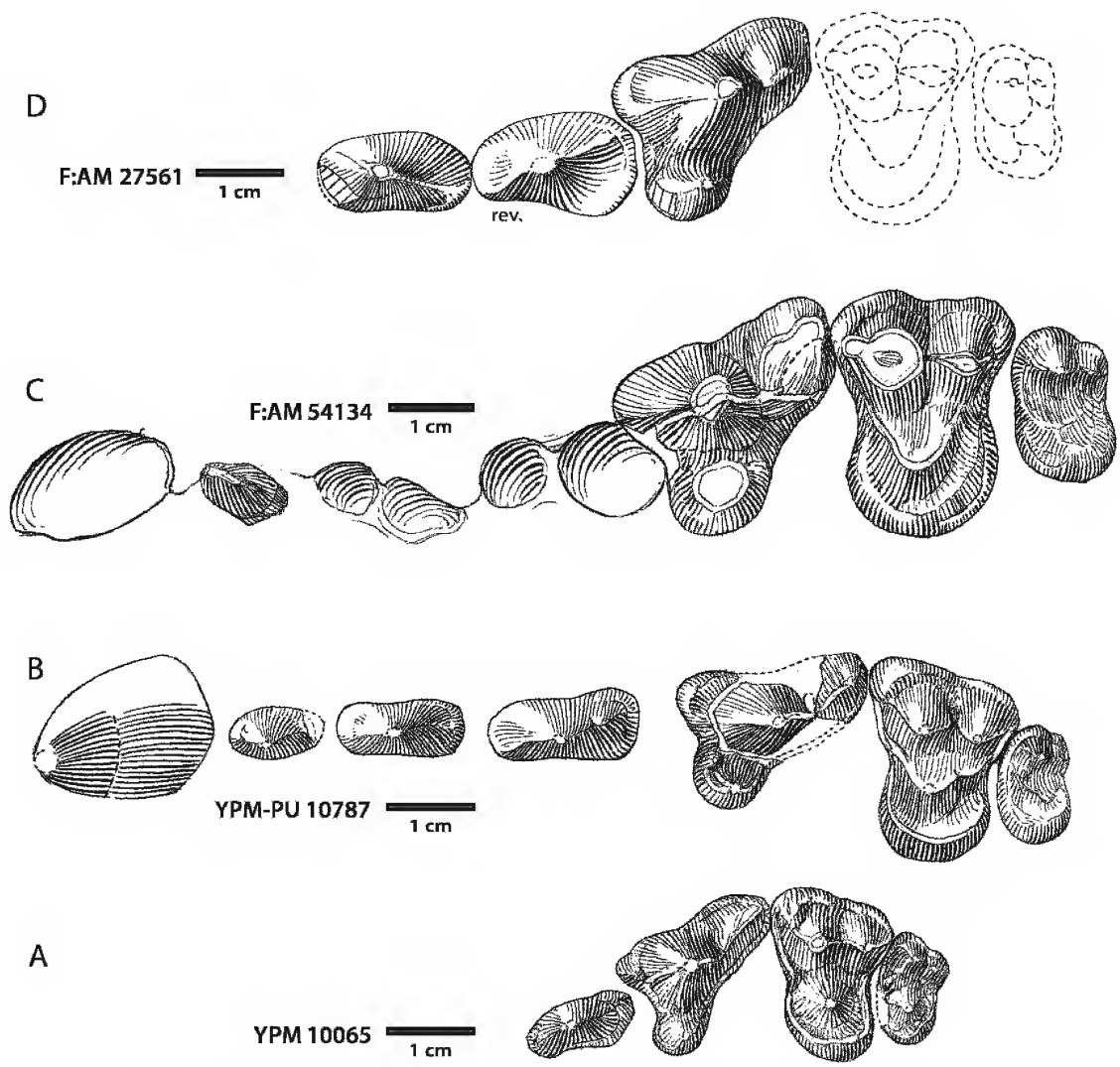


Fig. 43. Maxillary dentitions showing the development of a durophagous dental battery in temnocyonines: **A,** *Temnocyon subferox*; **B,** *Temnocyon ferox*; **C,** *Mammacyon ferocior*; **D,** *Delotrochanter major*.

the protocone region has begun to expand, although the P4–M1 embrasure remains fully functional. A shearing dental battery is still evident. M1 of *T. percussor* (fig. 15F) could be derived from the smaller *T. ferox* M1, and is lengthened lingually, whereas the M1 of *T. fingeruti* is little different from a scaled-up M1 of the Logan Butte *T. altigenis*. The M1 of *T. fingeruti* remains a relatively plesiomorphic molar (fig. 17).

The terminal species, *T. macrogenys*, displays enormous cheek teeth but the carnassial and m2 do not adopt the more modified occlusal form found in *Mammacyon* and *Delotrochanter*. The m1 and m2 of *T. macrogenys* retain metaconids and labially placed hypoconids (figs. 21, 44C), primitive features lost in the other genera (figs. 44A, B).

Species of *Temnocyon* remain dentally closer to the plesiomorphic dentition than other temnocyonines. On this basis they have been grouped together. The progressive size increase in these species as they undergo a gradual transformation of dental pattern over time lends support to this paraphyletic classification.

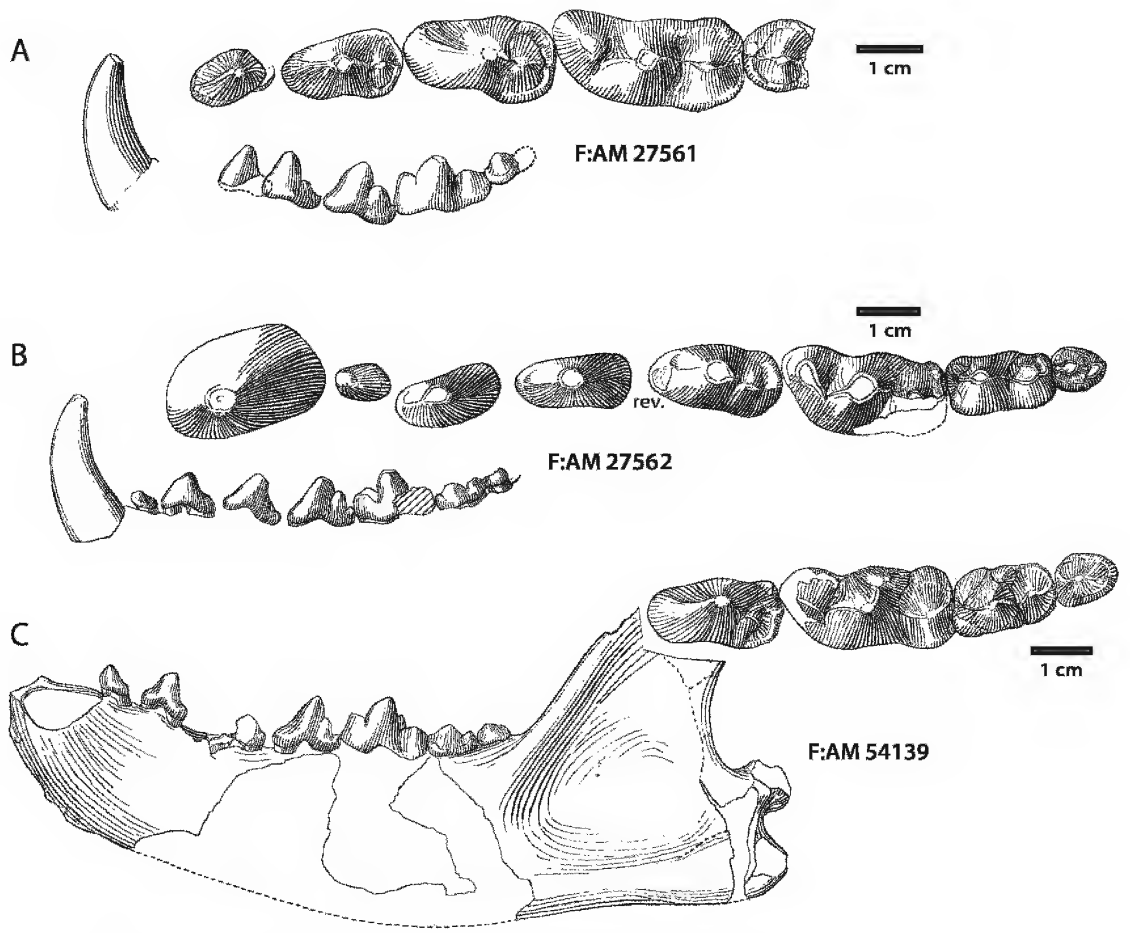


Fig. 44. Mandibular dentitions of the three terminal species of the genera *Temnocyon*, *Mammacyon*, and *Delotrochanter*: **A,** *Delotrochanter major*, F:AM 27561; **B,** *Mammacyon ferocior*, F:AM 27562; **C,** *Temnocyon macrogenys*, F:AM 54139.

In species of *Mammacyon* (*M. obtusidens*, *M. ferocior*, figs. 24, 27, 31, 43C) where the upper cheek teeth are preserved, the P3–M2 transform from the plesiomorphic state to a full-blown crushing dentition. In *M. obtusidens* some P4 shear remains, which is much less evident in *M. ferocior*. In these two species the P4 metastylar blade is shortened, the paracone becomes a tall, blunt cone, and the protocone a rounded, broad pestlelike cusp. M1 is now a crushing platform with a broadened lingual half (the protocone region), surmounted by a blunt, knoblike protocone. The P4–M1 embrasure is almost obliterated; hence the lower carnassial in these species chiefly crushes food against the P4 protocone/M1 lingual platform, although early in life some shear is present. This configuration is complemented by the shape of P3, whose heel widens (relative to species of *Temnocyon*) to form a platform for occlusion with the main cusp of p4.

The occurrence of the maxilla of *Mammacyon* (LACM 5386, fig. 27) in proximity to the dated Picture Gorge ignimbrite (~28.7 Ma) in Haystack Valley, Oregon, demonstrates that a crushing dental pattern had already developed in the early Arikareean, predating many of the less dentally derived species of *Temnocyon* in the John Day region.

Delotrochanter underwent a similar dental transformation resulting in crushing cheek teeth like those seen in *Mammacyon* (figs. 38, 39, 43D, 44A, 45A). However, upper cheek

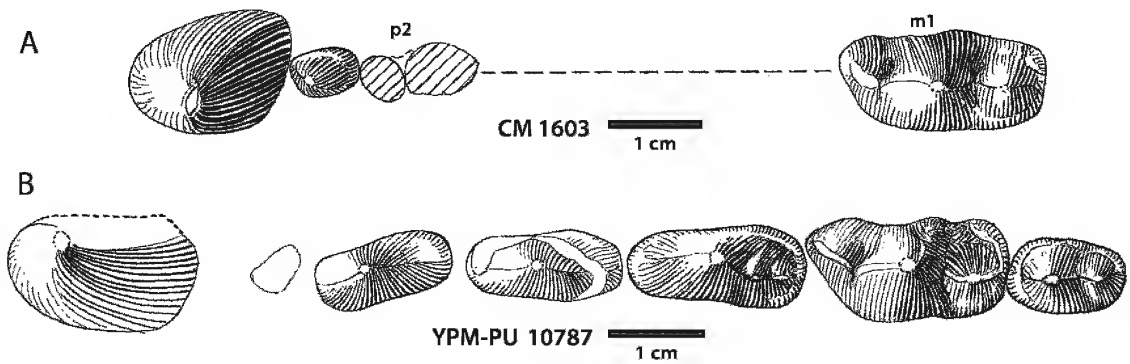


Fig. 45. Comparison of the lower carnassials of *Delotrochanter petersoni* and *Temnocyon ferox*, temnocyonines of similar size. The m1 metaconid has already been lost in *D. petersoni* (**A**), the earliest species of the genus, but is present in *T. ferox* (**B**). Note p2 alveolar diameters in (A).

teeth of *Delotrochanter* are unknown in the geologic record until *D. oryktes* occurs in the Harrison Formation at Agate National Monument, dated at ~22.9 Ma. *D. oryktes* and *D. major* share upper carnassials that duplicate the general form of the *Mammacyon* P4, together with the crushing platform on the adjacent P3 (the P4 protocone in *Delotrochanter* is never quite as developed as in *Mammacyon*). The *Delotrochanter* M1 is known only in *D. oryktes* (figs. 38, 39) where the lingual half of the tooth is broadened as in *M. obtusidens* but not to the extent evident in *Mammacyon ferocior*. Nonetheless, the dental batteries of both *Delotrochanter* and *Mammacyon* represent the parallel evolution of a type of crushing cheek teeth unknown in other living and extinct Carnivora. These durophagous dental batteries of *Mammacyon* and *Delotrochanter* are approached but not equalled by a few dentally similar European haplocyonine beardogs (Peigné and Heizmann, 2003; Bonis, 1973; Hürzeler, 1940; Helbing, 1928).

Measurements of the teeth support recognition of the four temnocyonine genera as distinct dental groups. Dimensions of M1 (fig. 46) reflect the expansion of the protocone region (relative to M1 length) that distinguishes *Mammacyon* and *Delotrochanter* from the more plesiomorphic *Temnocyon*. This same relationship is also evident when graphing M1 length against width (fig. 46). Also, P4 remains a narrower shearing carnassial in *Temnocyon* species, whereas it becomes a large crushing tooth, broadened by an enlarged protocone, in species of *Mammacyon* and *Delotrochanter* (fig. 47).

In the mandible, m1 dimensions suggest that this carnassial in species of *Delotrochanter* is slightly broader than in *Mammacyon* (fig. 48A); the m1s of the geologically youngest species of *Temnocyon* (*T. fingeruti*, *T. percussor*, *T. macrogenys*) seem narrow relative to length, reflecting retention of their primary role as shearing carnassials (table 2). *Mammacyon obtusidens* and *M. ferocior* mandibles are conspicuous for their elongated second molars. This is demonstrated by m2 length plotted against m1 length (fig. 48B) compared with the known examples of *Delotrochanter* and *Temnocyon* but especially with *Rudiocyon*.

These genera are also distinguished by premolar dimensions, notably the widths of p2, p3, and p4 (fig. 49). Invariably, broader premolars differentiate species of *Delotrochanter* from those of *Mammacyon*. The large species of *Temnocyon* generally fall between species of *Mammacyon* and *Delotrochanter*, and the dimensions of p2 and p4 seem to indicate an evident regression of length on width for *Temnocyon* species, a trend less obvious for p3. Van Valkenburgh (1989) noted the relationship of broad, robust lower premolars (measured as p4 "roundness") to a diet of meat/bone, a diet less dependent on meat alone.

The teeth of temnocyonines are unlike those of any living carnivore. Whereas the small stem temnocyonine, *T. altigenis*, differs little in dentition and body size from the plesiomorphic amphicyonid *Daphoenus vetus*,

the larger species evolve a unique combination of dental features. Large temnocyonines possess prominent canines and incisors, deep jaws, and broad snouts, features reported to be typical of large living canids that specialize in hunting prey larger than themselves (Van Valkenburgh et al., 2003). When combined with their tall, developed premolars, these traits argue for an ability to grasp and hold large prey. The deep jaws, strong mandibular symphysis, and canines are evidence of the strength and leverage of the bite. Rather blunt carnassials and broad molars add the capability to crush and grind hard food items during mastication.

CANINES: Temnocyonines have prominent canine teeth, capable of stabbing and lacerating. *Temnocyon altigenis*, the most plesiomorphic species, with a skull much smaller (75% of basilar length) than that of the living wolf, has already evolved proportionately large upper canines. The upper canine of *T. altigenis* (UCMP 9999) is long and robust (height 83% and basal area 89% of that of the wolf), whereas the lower canine falls at 83% and 62%, respectively.

Van Valkenburgh and Ruff (1987) have reported that the forces involved in the killing bite and handling of large prey are reflected in canine shape. I measured temnocyonine canines and compared this data with values obtained by Gittleman and Van Valkenburgh (1997) for large living carnivores of similar body mass (*Canis lupus*, *Crocuta crocuta*, *Panthera leo*, *P. tigris*, *Ursus arctos*). Measurements of height and basal canine diameters were taken on the lower canines of temnocyonines, since these, rather than the upper canines, were more often complete.

Canine bending strength was determined using the formulas of Van Valkenburgh and Ruff (1987) that estimate bending resistance around both the anteroposterior (AP) and mediolateral (ML) axes of the lower canine with canine height incorporated in these calculations: nine temnocyonines, three from each genus, were represented by intact teeth. Bending strength around the mediolateral axis (S_y) is commonly greater relative to the anteroposterior axis (S_x) in large living carnivores and also in temnocyonines (table 9). Species of *Temnocyon* show the lowest values, less than those of wolves for the small *T. altigenis* (the large *T. macrogenys* canine was not preserved). Species of *Delotrochanter*, regardless of body size, correspond closely to bending strength values of *Crocuta*, in keeping with the hyenalike skull form of *D. oryktes*. Species of *Mammacyon* fall between the spotted hyena and the large felids, indicating considerable strength of the lower canines.

Calculated bending strength of the few intact temnocyonine upper canines yielded similar estimates, suggesting comparable stresses to these teeth during predation and feeding. Four species preserve the upper canine (table 9). The small *Temnocyon altigenis* is similar to the much larger *Canis lupus*, particularly in resisting force applied to the sides of the canine; *T. ferox* closely parallels *Crocuta crocuta* in resisting both AP and ML stresses, whereas the upper canines of both *Delotrochanter oryktes* and *Mammacyon obtusidens* have S_x and S_y values that fall between those of the spotted hyena and the large cats, indicating strong resistance to forces applied at the symphysis.

Furthermore, many of the remaining upper canines, although broken off at the tip, retain the base in the alveolus. A proxy for canine shape was calculated using only the AP and ML diameters measured at the enamel-dentine junction at the base of the upper canine. Van Valkenburgh and Ruff (1987: fig. 3) plotted AP against ML diameters for living canids, felids, and hyaenids. As body size increased, the more mediolaterally compressed canines of large canids diverged from the more robust, less compressed canines of large felids and hyaenids. AP–ML upper canine diameters for temnocyonines plot with large felids and hyaenids, not canids (fig. 50A), suggesting ample resistance of their canines to mediolateral bending stresses. These authors thought that the greater strength of felid canines was related to their killing style, and for hyaenids to their bone-crushing habit. Canines of felids-hyaenids may strike bone during the bite, and then "be subjected to large oblique or mediolateral bending stresses" as the prey is subdued (Van Valkenburgh and Ruff, 1987: 391). Thus, both the upper and lower canines of temnocyonines, especially in the larger species, seem well adapted to stresses occurring during prey capture and feeding.

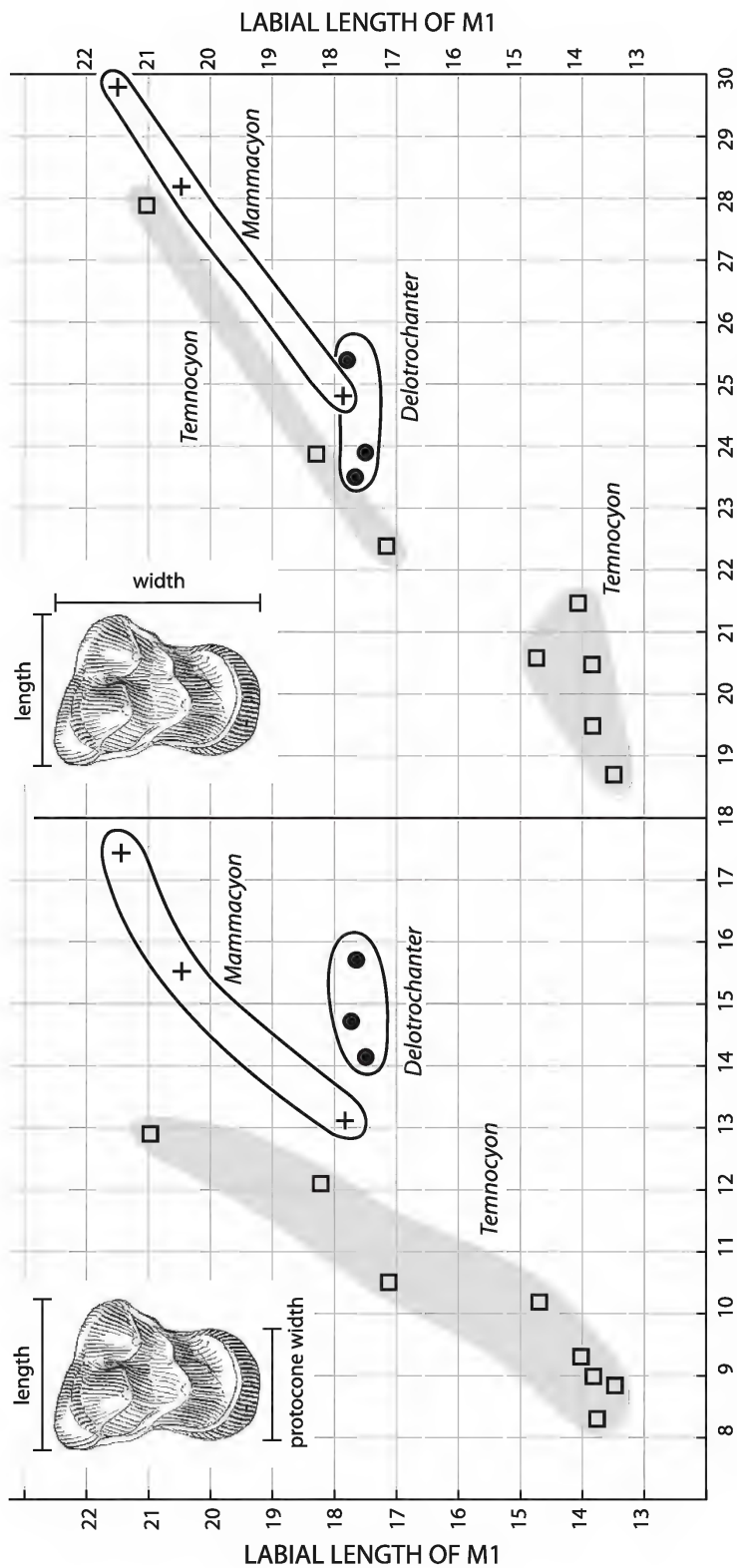


Fig. 46. Bivariate graphs of M1 dimensions (in mm) in North American temnocyonines. Lingual enlargement of the protocone region is interpreted as a durophagous adaptation distinguishing *Mammacyon* and *Delotrochanter* from *Temnocyon*.

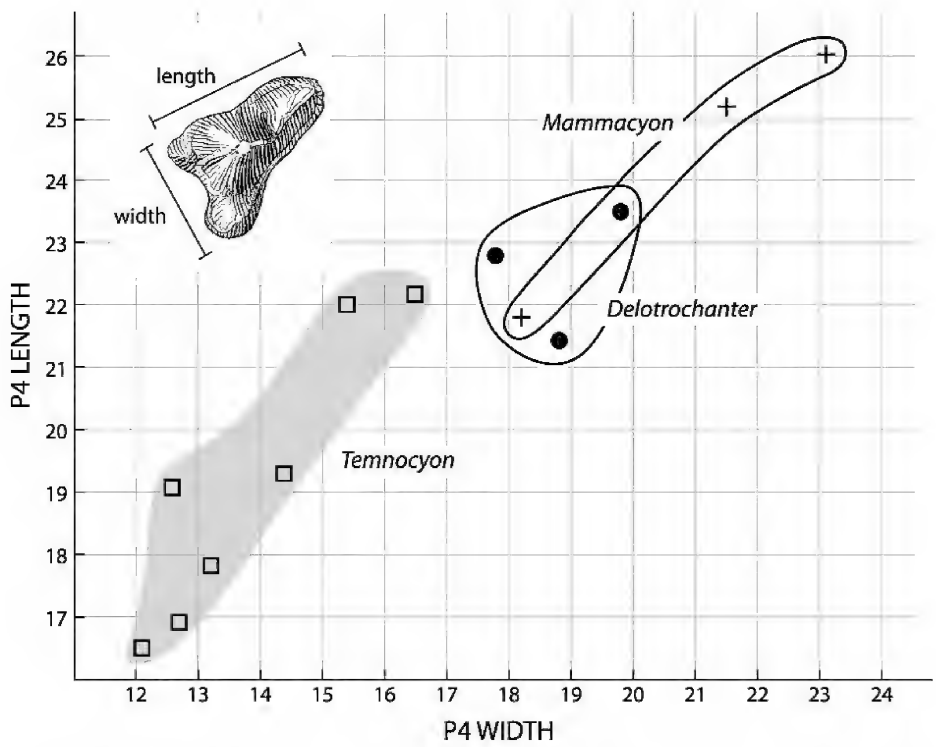


Fig. 47. Bivariate graph of P4 dimensions (in mm) of North American temnocyonines. Development of a crushing protocone increases P4 width in durophagous species of *Mammacyon* and *Delotrochanter*.

MANDIBLE: Mandibular dimensions of temnocyonines indicate considerable resistance of the jaws to bending stresses arising during mastication of hard materials and to forces applied at the front of the jaws during the kill. Jaws of some large temnocyonines such as *Temnocyon macrogenys* had apparently developed a parasagittal bending strength at the molars much greater than that of any living canid and similar to that of *Panthera leo* and *Crocuta crocuta*.

The resistance of the mandible to forces applied during feeding and prey capture has been examined in living carnivorans using several methods (Biknevicius and Ruff, 1992a, b; Van Valkenburgh and Koepfli, 1993; Biknevicius and Van Valkenburgh, 1996; Therrien, 2005). Biknevicius and Ruff (1992b) modeled the mandible as a hollow beam hinged at the jaw articulation, in which the distribution of cortical bone was calculated from biplanar radiographs. Mandibular cross-sectional geometry was first determined by examining actual cross-sections cut from the jaw, which were found to best approximate a hollow, asymmetrical cortical bone model. Using the radiographs, Biknevicius and Ruff (1992a) then calculated section moduli for canid, felid, and hyaenid mandibles to be used in determining mandibular bending strength. Alternatively, Therrien (2005) modeled the carnivoran mandible as a solid beam, recognizing that the solid beam method overestimates cortical bone cross-sectional area, which is better approximated using the method of Biknevicius and Ruff (1992b). Therrien (2005) showed that the solid beam approach, which lends itself to fossil material, could be used to represent *relative* differences in biomechanical properties along the mandible. Hence, differences among fossil and living species in terms of relative bending resistance along the mandible can be estimated and compared. The method assumes that the amount and distribution of cross-sectional cortical bone in such comparisons are similar, and that the individuals are of approximately the same body mass.

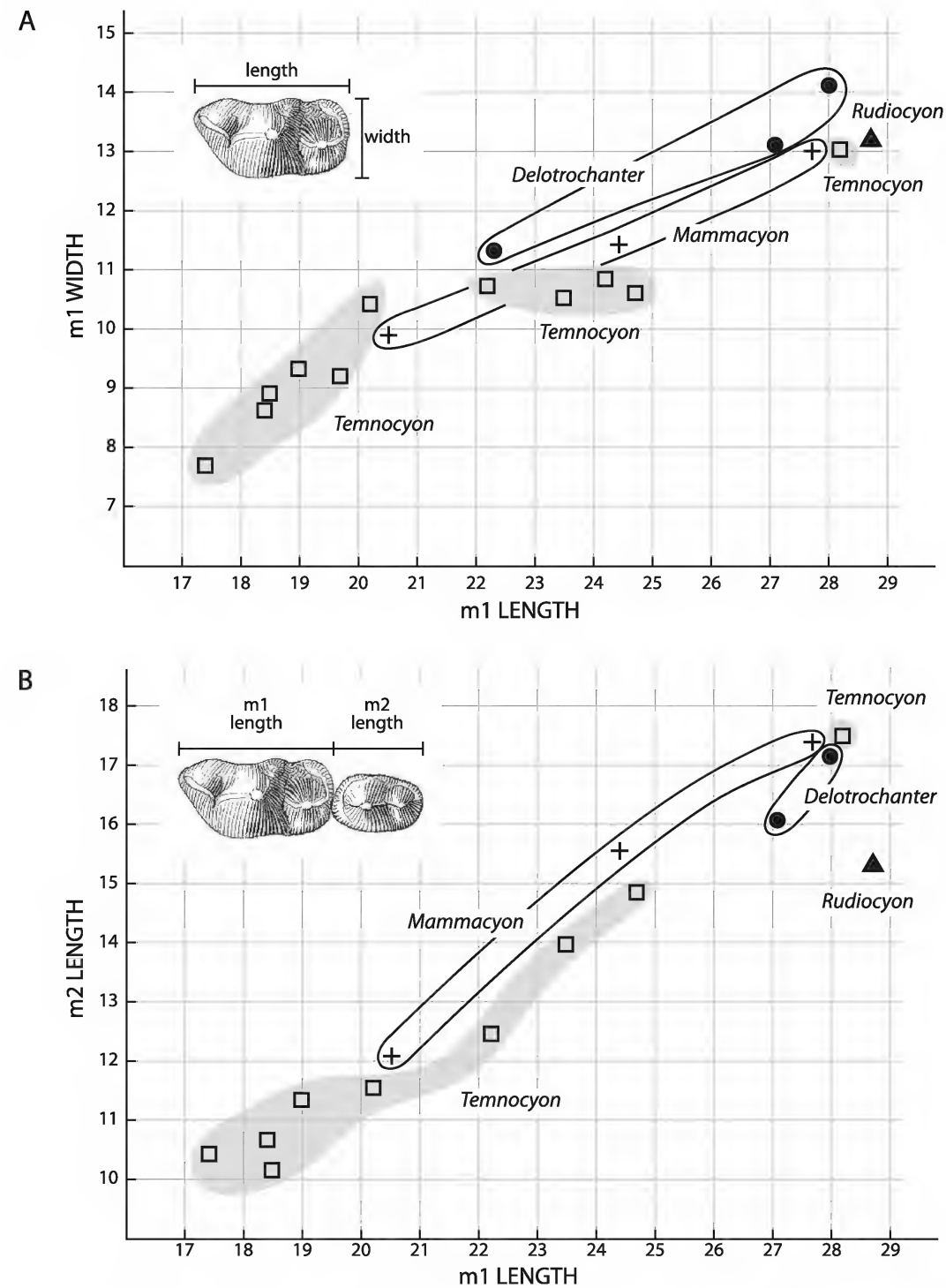


Fig. 48. Bivariate graphs of (**A**) m1 dimensions and (**B**) m1 length relative to m2 length (in mm) for North American temnocyonines, demonstrating a size increase during the Arikareean. Carnassial size (>27 mm) for the largest species of the four genera is similar in (A).

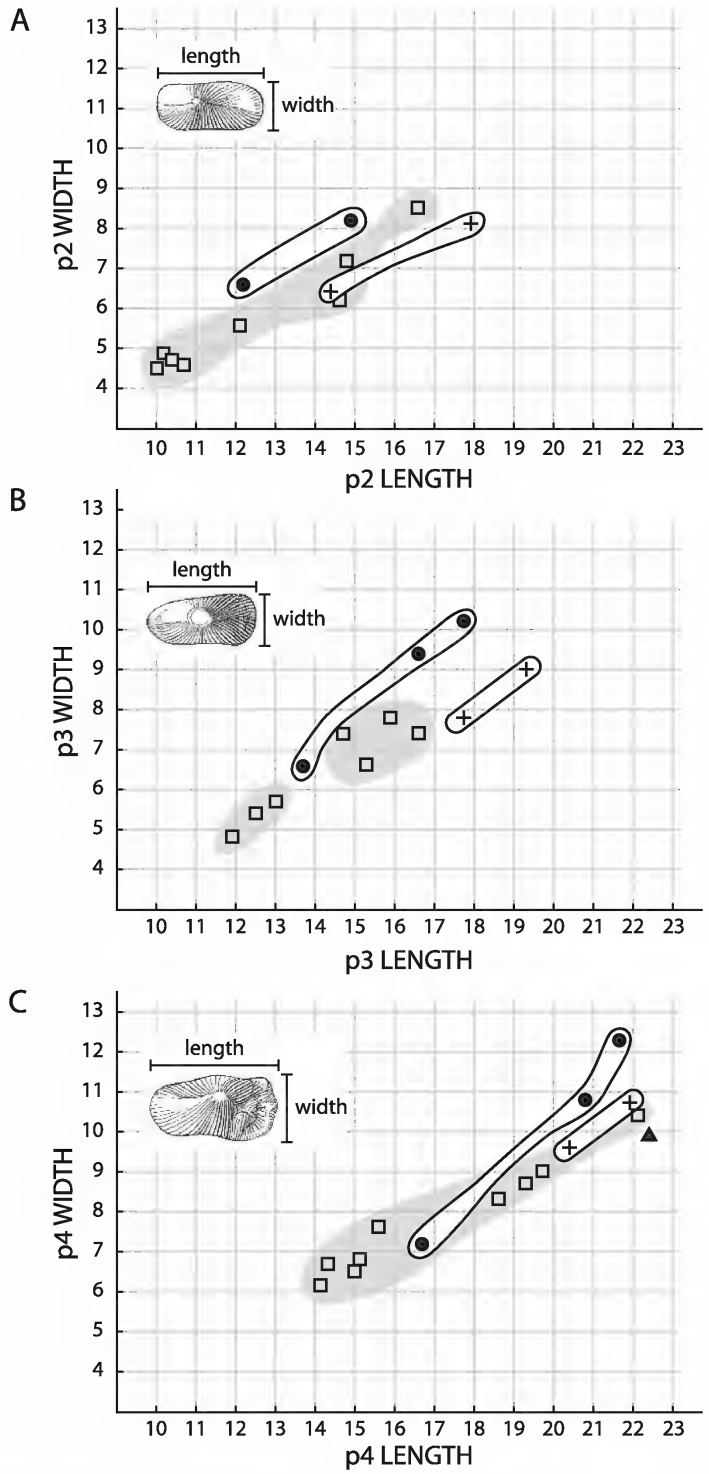


Fig. 49. Bivariate graphs of mandibular premolar dimensions (in mm) in North American temnocyonines. **A,** p2; **B,** p3; **C,** p4. Symbols for the genera are as in figure 48.

TABLE 9

Dimensions and Bending Resistance of the Upper and Lower Canines of Temnocyonines Relative to Living Carnivorans (in mm)

(S_x = $\log_{10}$ estimate of bending strength about anteroposterior axis of the canine; S_y = $\log_{10}$ estimate of bending strength about mediolateral axis of the canine.

	Mus. No.	Length	Width	Height	S_x	S_y
LOWER CANINE[a]						
Temnocyon altigenis	UCMP 9999	11.0	7.1	20.8	0.417	0.608
	AMNH 6856	11.1	8.2	~24	0.484	0.616
	AMNH 6855	12.5[b]	7.3[b]	—		
Temnocyon ferox	YPM-PU 10787	18.0	~11	37.2	0.759	0.973
Temnocyon fingeruti	NM 280/61	19.1	~10	—		
Temnocyon macrogenys	F:AM 54139	23[b]	14[b]	—		
Mammacyon obtusidens	LACM 9194	19.1	12.6	38.9	0.884	1.064
	ACM 34-41	22.1	14.1	~45	0.981	1.176
Mammacyon ferocior	F:AM 27562	20.3	14.0	~47	0.919	1.081
Delotrochanter petersoni	CM 1603	16.0	12.0	33.3	0.832	0.957
Delotrochanter oryktes	ACM 4804	18.5	12.5	36.8	0.887	1.057
Delotrochanter major	F:AM 27561	18.4	12.8	~40	0.869	1.027
Canis lupus	sample means[c]	13.9	9.1	25.0	0.655	0.839
Crocuta crocuta	sample means[c]	14.0	12.2	27.5	0.871	0.931
Panthera leo	sample means[c]	21.4	15.0	37.3	1.103	1.257
Panthera tigris	sample means[c]	21.3	15.8	42.1	1.093	1.223
Ursus arctos	sample means[c]	21.6	15.5	34.1	1.174	1.318
UPPER CANINE[a]						
Temnocyon altigenis	UCMP 9999	11.1	8.2	22.0	0.522	0.654
Temnocyon ferox	YPM-PU 10787	16.6	~12	37.3	0.799	0.940
Mammacyon obtusidens	ACM 34-41	22.1	14.2	48.0	0.960	1.152
Delotrochanter oryktes	ACM 4804	19.3	13.4	37.9	0.953	1.112
Canis lupus	sample means[c]	13.7	8.3	28.0	0.520	0.737
Crocuta crocuta	sample means[c]	15.1	11.2	29.6	0.798	0.928
Panthera leo	sample means[c]	23.1	16.7	45.1	1.147	1.288
Panthera tigris	sample means[c]	23.9	18.3	50.2	1.195	1.310
Ursus arctos	sample means[c]	21.3	15.7	36.2	1.153	1.286

[a]Length and width of canines measured at the base of the enamel.

[b]Alveolar measurement.

[c]Data from Gittleman and Van Valkenburgh (1997: table I), using the average of mean values for males and females.

These studies employed measurements taken from intact dentaries of living species. Temnocyonine mandibles are commonly incomplete, and almost all lack the ascending ramus with its processes and articular condyle that are essential to measurement of dentary length and the calculation of mandibular lever arms used to determine the mechanical advantage of jaw muscles (Van Valkenburgh and Koepfli, 1993; Van Valkenburgh et al., 2003). However, it was possible to approximate bending strength along the length of partial temnocyonine mandibles that preserved undamaged bone beneath the cheek teeth, using the solid beam model and external cross-sectional diameters measured at various points along the toothrow.

Mandibles providing the essential conditions for calculation of bending resistance survived in six temnocyonine species. Measurements were taken from two complete and four partial dentaries (appendix 2): Relative to dentaries in living carnivorans, estimated temnocyonine dentary lengths indicate that the small *T. altigenis* is similar to *Canis latrans*; *Temnocyon ferox*, *T. fingeruti*, and *Mammacyon obtusidens* approximate *Canis lupus*; and the large *T. macrogenys* slightly exceeds *Panthera leo*, whereas *D. oryktes* is most like *Crocuta* in form but of greater

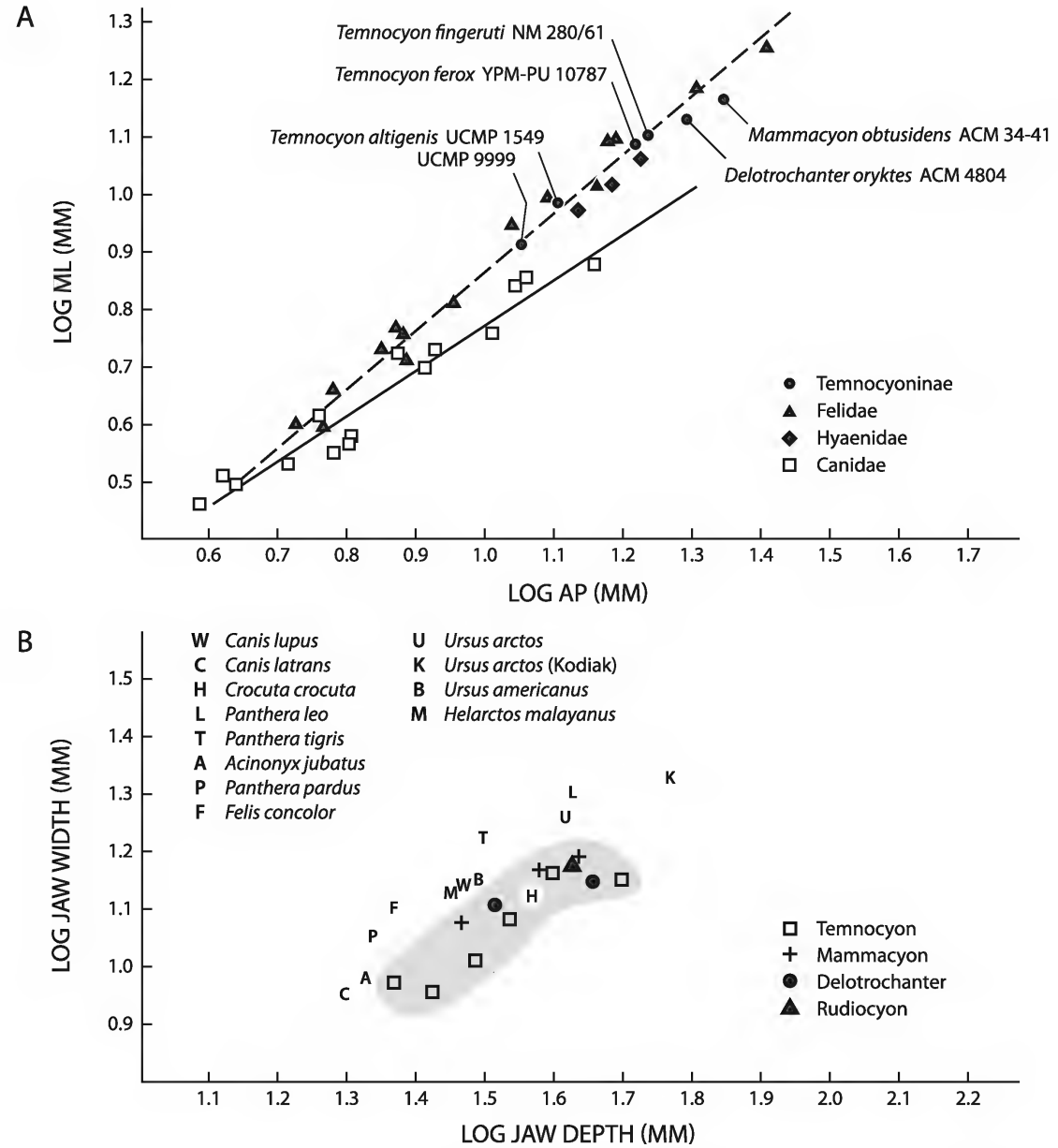


Fig. 50. (**A**) Log-log plot of upper canine anteroposterior diameter (AP) against mediolateral diameter (ML) as calculated by Van Valkenburgh and Ruff (1987: fig. 3) from samples of living felids, hyaenids, and canids. Temnocyonines plot with felids and hyaenids, not canids; (**B**) Log-log plot of mandibular depth against width in large living carnivores and temnocyonines (table 10): measured below m1–m2 interdental gap in canids and temnocyonines; below m1 in felids and *Crocuta*; below m2 in ursids.

length. Calculation of bending resistance depends on the length of the working side lever arm (the distance from the point of application of force along the toothrow to the jaw articulation). This length (L) was estimated for the partial dentaries and accurately determined for the two complete jaws. The m1m2 interdental gap was selected as the bite locus (point of applied force). Temnocyonines have a proportionately lon-

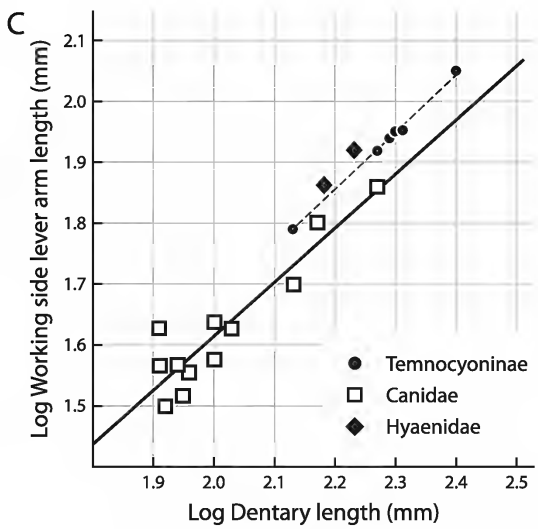


Fig. 50 (*continued*). (**C**) Log-log plot of dentary length relative to working side lever arm length (articular condyle to m1/m2 interdental gap for canids and temnocyonines; to p4/m1 for hyaenids). Canid-hyaenid data and regression from Biknevicius and Ruff (1992a: fig. 9A).

ger working side lever arm than those of large living canids (fig. 50C). This appears to be the result of lengthened crushing surfaces of molars used to process hard material, a probable adaptation for durophagy.

Many temnocyonines seem to have dorsoventrally deep, labiolingually narrow mandibles. When temnocyonine mandibular width is plotted relative to depth, it is apparent that these beardogs possess deep, narrow mandibles when compared with those of living carnivores of similar body size (fig. 50B). When bite force is applied to the principal cheek teeth during mastication, these temnocyonine mandibles are able to resist substantial dorsoventral bending stress. Jaw depth measured below m1–m2 for large species of *Temnocyon* (~35–53 mm), *Mammacyon* (~38–44 mm), and *Delotrochanter* (~46 mm) corresponds to, and in some cases exceeds, values (29.8–43.3 mm) observed for *Canis lupus*, *Panthera leo*, *Crocuta crocuta*, and *Ursus arctos* at functionally analogous points on the mandible (table 10).

To further explore the relationship between mandibular structure and jaw function, the two intact temnocyonine mandibles (*Temnocyon macrogenys*, F:AM 54139; *Delotrochanter oryktes*, ACM 4804) were compared with a representative canid (*Canis lupus*), hyaenid (*Crocuta crocuta*), and felid (*Panthera leo*), carnivores that approximate the size range of these large temnocyonines (appendix 3). Included here for its heuristic value is the largest known daphoenine amphicyonid, *Daphoenodon (Borocyon) robustum*, from the early Miocene Runningwater Formation of Nebraska, a carnivore comparable in body size to the large temnocyonines (Hunt, 2009).

The two temnocyonine mandibles were oriented and measured according to Therrien's (2005: 252f.) method of beam analysis. Mandibular depth and width were measured in centimeters with dial calipers at interdental foci between p3p4, p4m1, m1m2, m2m3, and directly behind m3 (post-m3). Depth of the mandibular symphysis was measured as a vertical posterior to the canine; mandibular width was measured from a point on the labial face of the mandible directly behind the canine to the posterior termination of the symphysis (Therrien, 2005: fig. 2, canine). Working side lever arms were calculated as the distance from the articular condyle to the various interdental points along the mandibular corpus. Dentary length was taken as the distance from articular condyle to the mandibular terminus directly anterior to the canine (Biknevicius and Ruff, 1992a: fig. 1). These measurements on temnocyonine jaws were then compared with sample means for the various species of canids, hyaenids, and felids provided by Therrien (2005: figs. 3–7, appendices 1, 2).

Despite its limitations in overestimating the amount of cortical bone in cross-sections, the solid beam model allowed comparison of relative patterns of bending strength along the mandibles of both the fossil and extant species. Second moments of area (Iy, Ix), which estimate the cross-sectional distribution of cortical bone about the dorsoventral and labiolingual axes, were calculated from the formulas of Therrien (2005: 250). From these were derived the section moduli, Zx and Zy, which are respective measures of parasagittal and transverse bending strength. These moduli are a reflection of bending moments applied to the mandible during prey capture and feeding.

The bending resistance of a point along the mandible during the bite is a function of the

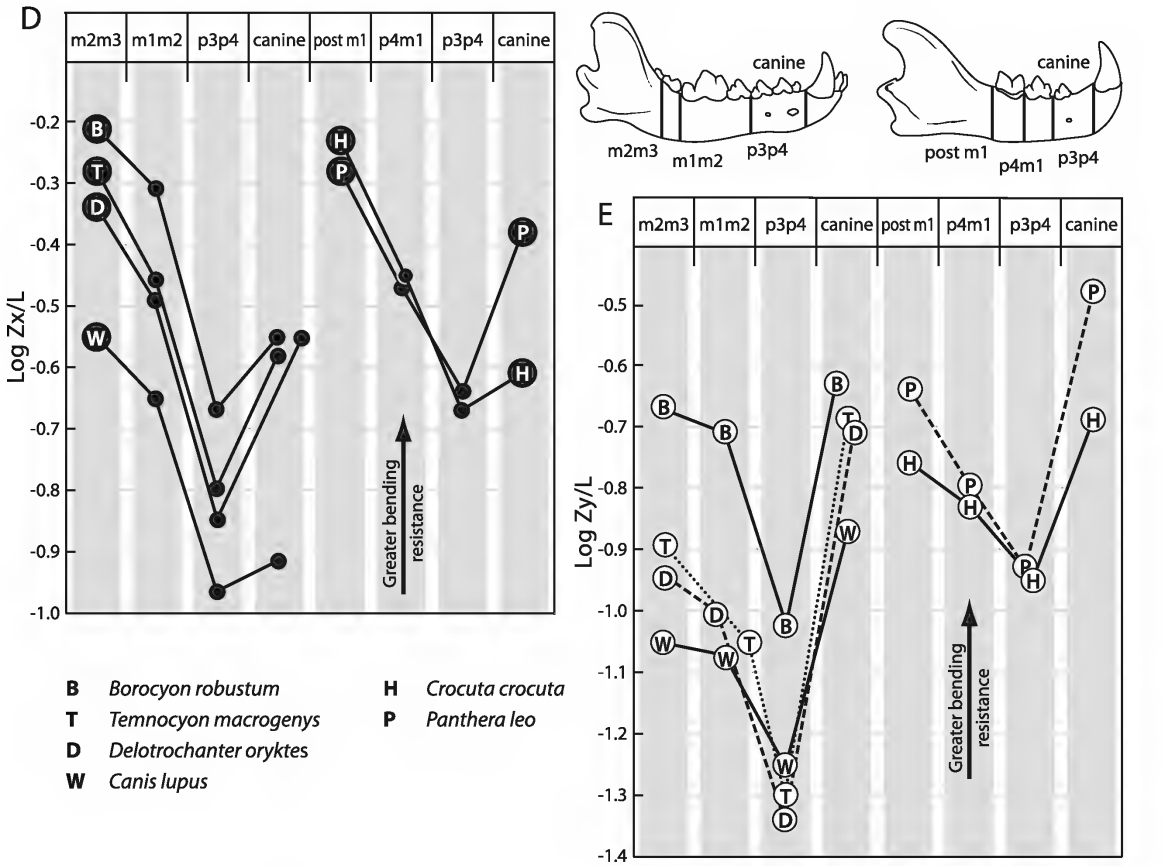


Fig. 50 (*continued*). (**D**) Magnitude of dorsoventral force (Zx/L) applied at interdental loci along the mandible. Zx, the section modulus, measures parasagittal bending strength relative to length (L) of the working side lever arm. (**E**) Magnitude of labiolingual force (Zy/L) applied at interdental loci along the mandible. Zy, the section modulus, measures transverse bending strength relative to length (L) of the working side lever arm. Diagrams of caniform and feliform mandibles show location of linear measurements taken at interdental gaps. Data for canid, felid, and hyaenid from Therrien (2005).

distance (L) from the articular condyle to a particular dental locus, which is then expressed here as a ratio to derive parasagittal (Zx/L, fig. 50D) or transverse (Zy/L, fig. 50E) bending strength values. These graphs compare patterns of bending strength along the various caniform and feliform mandibular corpora, providing insight into relative bending moments typical of these species.

Living carnivores studied by Therrien (2005: figs. 3–7) typically show parasagittal bending strengths at the various post-canine loci along the mandibular corpus to be greater than transverse values. The temnocyonines and the daphoenine *Borocyon robustum* show clear parallels here to the large living canids in bending strength values distributed along the mandible, which rise rapidly distad along the mandible from p3p4 to directly behind m3. The daphoenine and temnocyonines share with these canids (*Canis lupus*, *Lycaon pictus*, *Canis rufus*) a crushing molar platform (m1 talonid, m2–3) and similar ZxL and ZyL force profiles in which maximum bending strength occurs in proximity to the molars at the back of the jaw (figs. 50D, E). These amphicyonids, however, show much greater bending strength at the molars and a longer crushing platform relative to canids studied by Therrien (2005: fig. 6).

The mandibular force profile of *Borocyon robustum* far exceeds the values for any living canid, and also the extinct *Canis dirus* (Therrien, 2005: fig. 6). *Borocyon robustum* is

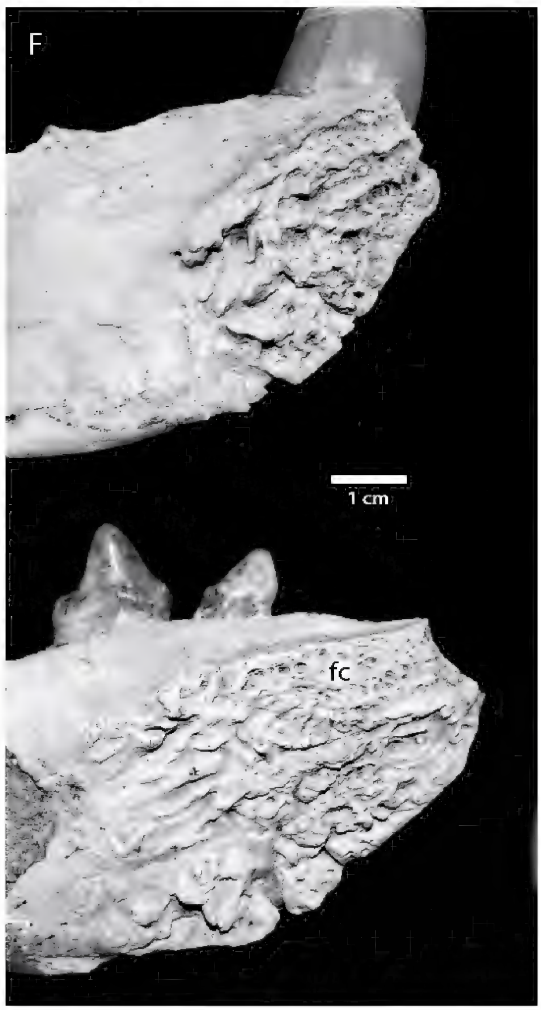


Fig. 50 (*continued*). (**F**) Mandibular symphyses of *Delotrochanter oryktes* (top) and *Temnocyon macrogenys* (bottom). Interdigitating rugose bone and ligaments strengthen these mandibular symphyses against forces encountered during prey capture and feeding; note area for fibrocartilage pad (fc) in *T. macrogenys*.

a much larger animal with more massive jaw musculature than a typical wolf, thus the greater bending strength values are likely due in part to the size of this daphoenine. However, resistance to bending at the canines is much greater than in the wolf, evident in the beardog's more strongly buttressed mandibular symphysis (Hunt, 2009: fig. 38), resistant at the canines to both parasagittal and transverse forces applied during prey capture and feeding. Known from its skeleton to be a cursorial predator, *B. robustum* appears to have had an ecologic role as a large wolflike hypercarnivore able to easily process bone and other tough fibrous foods (Hunt, 2009).

Higher Zx/L and Zy/L values for *Temnocyon macrogenys* and *Delotrochanter oryktes* reflect their greater body size and more massive jaw musculature relative to the large living canids. The largely parallel patterns of bending resistance along the toothrow, however, indicate a similar distribution of applied force along the mandibular corpus during feeding, except for the canines and mandibular symphysis. Zy/L values show temnocyonine mandibles to be stronger at the canines when subjected to transverse stresses, than at the molars, which Therrien (2005) interpreted as an indication of substantial torsion at the symphysis.

Temnocyonines and *Borocyon* are exceptional in their Zx/L and Zy/L values for parasagittal and transverse bending strength at the canines/mandibular symphysis. They compare with the spotted hyena (figs. 50D, E), yet cannot match the considerable parasagittal and transverse strength achieved by the lion. The wolf and other large living canids have lower values for canine/symphyseal bending strength, possibly explained by the quick, sharp nipping bites used by social pack-hunters to bring down large prey without the stresses encountered by lion and spotted hyena in capturing and feeding on large ungulates. The reinforced symphysis of these temnocyonines (fig. 50F) and *Borocyon*, composed of two rugose interlocking mandibular plates joined by strong ligaments, better resists torsional forces than the symphysis of the wolf. The broader, more rectangular form of the *T. macrogenys* and *B. robustum* symphyses is evident in their length/width ratios (1.51, 1.48, respectively; *Mammacyon ferocior*, 1.41; *M. obtusidens*, 1.45) relative to the narrower, elliptical symphyses of *Delotrochanter oryktes* (2.15) and *Crocuta crocuta* (~2.7–2.9).

Zx/Zy values are a measure of *relative* bending strength about the sagittal and transverse planes of the mandibular corpus (Biknevicius and Ruff, 1992a: 484), considered by Therrien (2005) as mandibular force profiles. These Zx/Zy ratios (fig. 50G, appendix 3) estimate the relative differences

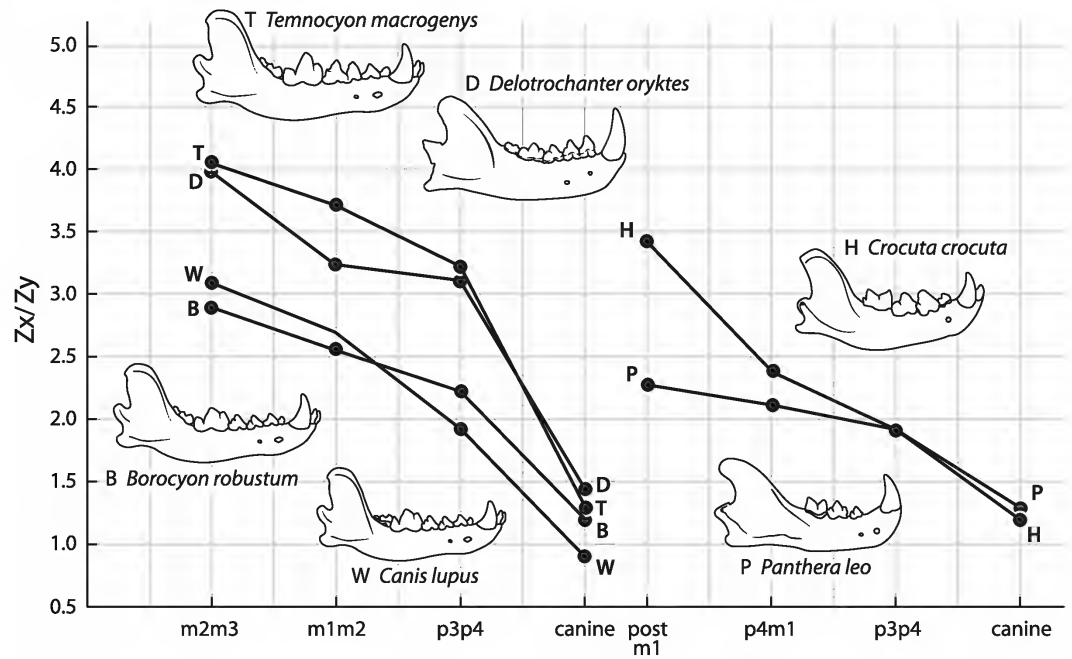


Fig. 50 (*continued*). (**G**) Mandibular force profiles (Zx/Zy) of caniform and feliform carnivorans. Zx/Zy values are nearly all >1.0, indicating greater bending resistance to dorsoventral relative to labiolingual stresses applied at mandibular loci during prey capture and food processing. The temnocyonines show exceptional parasagittal bending resistance below the molars that reflects their deep, narrow mandibles at this locus. Zx/Zy canine ratios (1.2 to ~1.5) of the three amphicyonids, *Crocuta crocuta*, and *Panthera leo* are comparable, indicating similar resistance to stresses at the mandibular symphysis.

between parasagittal and transverse loadings along a single mandible with the advantage that these patterns can then be compared among carnivoran species. The temnocyonine pattern of Zx/Zy ratios along the mandibular corpus indicates the ability to tolerate heavy dorsoventral loading at the molar platform. Thus, temnocyonines combine great strength at the canines and symphysis to hold and dispatch prey with powerful forces exerted at the molar battery to grind and crush hard food material during feeding. Living large canids have been observed chewing hard food items, including bone, at this molar locus (Mech, 1970; Haynes, 1982; Van Valkenburgh, 1996), and temnocyonines also possessed this capability.

Addition of bone (buttressing) is to be expected in the mandibular corpus reinforcing dorsoventral and labiolingual as well as torsional bending strength when strong forces are applied to the teeth during feeding and prey capture. Particularly strong loadings are anticipated where teeth are used to comminute hard, tough foods. In their analysis of living canids and hyaenids, Biknevicius and Ruff (1992a: 497) observed that the location along the mandible of teeth used to chew hard foods (primarily in bone-processing) seemed to determine durophagous adaptations: increased bending strength materialized directly caudal to bone-processing teeth. In temnocyonines, precarnassial teeth seem less involved in masticating bone or other hard food items, evidenced by less apical wear on anterior premolars (P1–2, p1–3), while cusps of P3–M2 and p4–m3 show blunt wear, a situation similar to that known in wolves. The posterior cheek teeth of temnocyonines, notably in the large dentally derived species, were uniquely specialized for crushing and grinding hard material. Bone processing by temnocyonines, relative to living canids, may have been favored by the longer working side lever arm at the molars (fig. 50C) that apparently accommodated a somewhat wider gape.

The two temnocyonines (*T. macrogenys, D. oryktes*) in which intact mandibles sur-

TABLE 10
Mandibular Measurements of Temnocyonines and Living Carnivorans (in mm)

	Mus. No.	Jaw depth[a]	Jaw width
Temnocyon altigenis	AMNH 6855	30.7	10.3
	AMNH 6856	26.8	9.0
	UCMP 9999	23.3	9.2
Temnocyon fingeruti	NM 280/61	34.5	~12–13
Temnocyon ferox	YPM-PU 10787	39.6	14.5
Temnocyon macrogenys	F:AM 54139	~50–53	14.2
cf. *Mammacyon* sp.	LACM 15908	29.7	11.9
Mammacyon obtusidens	LACM 9194	~38	14.5
Mammacyon ferocior	F:AM 27562	~44	15.4
Delotrochanter petersoni	CM 1603	32.8	12.9
Delotrochanter oryktes	ACM 4804	45.6	14.0
Rudiocyon amplidens	LACM 480	43.0	15.3
Canis latrans	N = 12[b]	20.3[c]	8.9[c]
Acinonyx jubatus	N = 4	21.6	9.7
Panthera pardus	N = 1	22.0	11.2
Felis concolor	N = 8	23.6	12.7
Helarctos malayanus	N = 1	29.0	13.7
Canis lupus	N = 11	29.8	13.8
Ursus americanus	N = 2	30.9	14.1
Panthera tigris	N = 6	31.8	16.8
Crocuta crocuta	N = 2	36.9	13.3
Ursus arctos	N = 4	41.3	18.0
Panthera leo	N = 3	43.3	20.2
Ursus arctos (Kodiak Is.)	N = 1	59.0	21.4

[a]Measured below m1 in felids and *Crocuta*; below m2 in ursids; below m1–2 interdental gap in *Canis lupus*, *C. latrans*, and temnocyonines.

[b]N, sample size for living carnivorans.

[c]If N>1, values are means for living carnivorans.

vived must have differed considerably in external appearance (figs. 20, 34). Although much larger, the elongate mandible of *T. macrogenys* is shaped like that of *Canis lupus* and indicates a rather long "doglike" skull. *Temnocyon macrogenys* must have been an enormous wolflike predator with a long-legged striding gait and other predictable cursorial features. The shape of the *D. oryktes* mandible is hyenalike; the skull short with broad snout and deep zygomata much as in *Crocuta*, although lacking the wider palate of the hyena. The form of its blunt-cusped cheek teeth are unlike those of living canids and hyaenids, yet doubtless served a crushing function, in agreement with pronounced mandibular buttressing along the ventral margin of the jaw below the cheek teeth. The large species of *Delotrochanter* appear to be temnocyonines that, to some extent, craniodentally parallelled the bone-crushing hyaenids.

POSTCRANIAL OSTEOLOGY: THE FIRST LARGE CARNIVORAN CURSORS

In temnocyonine beardogs, lengthening of the limbs and adoption of a more upright stance accompanied by skeletal modifications promoting a more restricted fore-aft motion of the limb and foot are evident adaptations influencing the gait, stride, and energy budget of these archaic carnivorans.

Longer limbs are associated with living cursorial carnivores, particularly the larger canids such as wolves (*Canis lupus*) and the African hunting dog *Lycaon*. Here endurance coupled with pack hunting behavior during a prolonged pursuit replaces the hunting strategy of the solitary carnivore that relies on rapid acceleration and attack speed. This capability is manifest in musculoskeletal and physiological adaptations that maximize energy savings. Predatory cursors optimize gaits

that minimize energy costs (Alexander, 2003). The preferred pursuit gait is a compromise that conserves energy while outlasting the prey—to achieve this, speed, acceleration, maneuverability, and locomotor stability are mutually adjusted within the physiological and structural capability of the carnivore.

Lengthening the limbs, particularly the lower limb and foot, are essential to the endurance strategy, increasing stride and step length. Research on mechanical design in mammals also suggests a benefit to the more upright stance that often accompanies lengthening of the limbs (Biewener, 1989a, b). Energy is further conserved by concentrating muscle mass in the proximal limb segments, thereby reducing the limb's moment of inertia and the energetic cost of locomotion (Myers and Steudel, 1985); thin, distal tendons transmit the force of a much thicker proximally placed muscle while effectively reducing the mass of the lower limb.

Economy of motion is also achieved by confining the limb to a fore-aft path. An indication of restricted fore-aft motion is often evidenced by closely registered joint surfaces in the lower limb segments—this registration can be seen in the hind limb of living cursorial canines in the interlocked fit of astragalus and calcaneum; by close apposition of the metapodials; by pronounced keels on the distal metapodials for the sesamoids and proximal phalanges; and by a deeply grooved astragalar trochlea firmly inserted in the distal tibia-fibula. In the forelimb a more erect stance and fore-aft motion are achieved by parasagittal alignment of the limb in which the scapula functions as the upper mobile segment of the forelimb; by reducing or eliminating angulation at the elbow; by a constrained articulation of the ulna with the humerus favoring fore-aft excursion; by reduced participation of the distal ulna in the carpal joint of the wrist; and by modifications of carpal bones, metacarpals, and phalanges that promote stability during protraction and retraction of the forefoot. In both fore- and hind limb a digitigrade stance allows energy storage in tendons and ligaments supporting the feet (spring mechanisms)—strain energy is thereby stored and released during each stride. A number of these skeletal adaptations are evident in temnocyonines, although in some species not developed to the extent seen in a living cursorial canid such as the wolf.

In living canine cursors and in temnocyonines the potential use of the forelimb in prey capture is sacrificed to the efficient fore-aft gait, a compromise favoring endurance, and accompanied in wolves and African hunting dogs by reliance on pack hunting. Sustained gaits of this type must be powered by aerobic locomotion, and since the metabolic rate of active striated muscle achieves maximum efficiency at a speed of contraction somewhat less than the speed of maximum power output (Alexander, 2003), a gait such as the sustained trot seems well adapted to endurance pursuit in these cursors.

Heglund and Taylor (1988) observed that terrestrial mammals prefer speeds falling in the mid-range of a particular gait such as the trot and gallop. Although the preferred speeds of these mammals increase with body size, stride frequency decreases, accompanied by a mass-specific decrease in energy cost, which suggests that there is an advantage to increasing body size in a cursorial carnivore. Hildebrand (1962) reported that as speed increases, living ungulates and carnivores increase stride length considerably but increase stride frequency only slightly, a plausible strategy for energy conservation. This must be balanced against the cost of acquiring the available (finite) resources necessary to maintain the body mass of a larger animal.

The temnocyonine skeleton represents the earliest experiment by large species within the Order Carnivora at lengthening the limbs (proportionally longer lower limbs and feet), approaching cursorial canids in this regard, as evidenced by the humeroradial and femorotibial length ratios, and by elongation of the metapodials and digits of the feet (tables 8, 11, 12). The close registration of the joint surfaces of the distal limbs did not progress to the same degree found in cursorial wolves and coyotes, but the first attempts at this are evident in temnocyonine tarsal structure and in the apposition of the metapodials, accompanied by reliance on the paraxonic foot with greatly reduced metapodials 1, 2, and 5. A straight-legged digitigrade stance accompanies these adaptations, marked by less angulation at the elbow

evidenced in the deep penetration of the head of the ulna into the olecranon fossa of the humerus, creating in some species a perforate fossa of the type seen in living canids. The transversely narrow distal humerus with deep symmetrical olecranon fossa so typical of the erect stance of wolves and coyotes is present even in the earliest temnocyonines. Prominent scars along the shafts of radius and ulna show that these bones were joined by strong interosseous ligaments that in the younger derived species may have limited rotation of the radius on the ulna.

In the larger temnocyonines where the forelimb has survived (*Mammacyon obtusidens*, *M. ferocior*, *Delotrochanter oryktes*), the radius, ulna, and metapodials are lengthened, resulting in an elongate forelimb. Pronation-supination of the forelimb involving rotation of radius on ulna is restricted, yet not to the degree evident in the wolf. Rotation of the radial head in the radial notch of the ulna is not as limited in these beardogs. However, the articulation of the distal ulna with the radius and carpus is as advanced as in the wolf. In both wolf and beardog the radial process of the distal ulna is reduced to a flat articular facet appressed tightly against the radius that permits only limited movement. Whereas some mobility remains in the wrist in the articulation of the proximal carpals (scapholunar, carpal cuneiform) with the radioulna, the rotation of the radius is certainly diminished, indicating restriction of the forelimb to a more fore-aft trajectory. The elongate paraxonic fore- and hind feet, a digitigrade stance, and reduction of the lateral digits in these large temnocyonines further suggest a mobile cursorial predator.

Temnocyonine Postcrania

Postcranial remains have rarely been found with crania or dentitions of temnocyonines. However, five species are now known to have postcranial elements associated with dentitions (table 8). At least one species in each of the three principal genera recognized in this study is represented by a significant portion of the postcranium.

In the John Day beds of Oregon, *Temnocyon altigenis* is known from a partial skeleton from Logan Butte (Merriam, 1906) and *Temnocyon ferox* is represented by the nearly complete skeleton described by Eyermann (1896). This latter species is considerably larger and younger than *T. altigenis*. These two skeletons demonstrate that some cursorial traits retained in *T. ferox* had already developed in *T. altigenis*, arguably the oldest and most plesiomorphic temnocyonine.

In the Great Plains the postcranial skeleton of *Mammacyon* is known from limited material belonging to the holotype of *M. obtusidens* and from a more complete skeleton of the larger, more advanced *M. ferocior*. *M. ferocior* represents the terminal species of its lineage and demonstrates the postcranial adaptations that accompanied a robust crushing dentition—this species displaying the most extreme example of durophagy in the Temnocyoninae.

The quarries at Agate Fossil Beds National Monument have produced two individuals of *Delotrochanter oryktes,* one from *Stenomylus* Quarry (Loomis, 1910: 298), and the other from the carnivore dens at Beardog Hill (Hunt et al., 1983; Hunt, 1984). These are the only individuals in this genus with associated skeletons, and they reveal the most extreme cursorial modifications of the feet yet recognized in temnocyonines.

Without question the single characteristic distinguishing the temnocyonine skeleton is the change from the primitive skeletal proportions of an early amphicyonid such as *Daphoenus* to the cursorial stance evident in the limbs and feet of temnocyonines. These altered proportions occur in all three genera and demonstrate a somewhat diachronous yet clearly parallel evolution of cursoriality during the Arikareean NALMA.

Dimensions of the temnocyonine postcranial skeleton (table 8) can be established for two species of *Temnocyon*, two of *Mammacyon*, and one species of *Delotrochanter*. This record of the postcrania in these five species is particularly fortuitous in demonstrating that cursorial modifications in the limbs and feet occur in each of the principal lineages of the subfamily.

Proportions of the forelimb (humerus, radius) are better known than for the hind limb (femur, tibia) because the femur in several cases was not complete or did not

TABLE 11
Limb Proportions of Temnocyonine, Daphoenine, and Amphicyonine Amphicyonids

Mus. No.	Humerus	Radius	R/H	MC4	Femur	Tibia	T/F	MT4
TEMNOCYONINAE								
Temnocyon altigenis								
UCMP 9999	159[a]	~132	83.0					
Temnocyon ferox								
YPM-PU 10787	206	186	90.3	71.6	244	222	91.0	84.3
Mammacyon obtusidens								
ACM 34-41	217	~205	94.5			~239		85.0
Mammacyon ferocior								
F:AM 27562	247	227[b]	91.9		~275	265	96.4	
Delotrochanter oryktes								
ACM 4804	220	210	95.4		246	228	92.7	88
ACM 4804A[juv]		166			207			
UNSM 47800				83.9				91.0
DAPHOENINAE								
Daphoenus vetus								
F:AM 25451	142	119	83.8					62.4
USNM 17847	160	125	78.1					
F:AM 76206	159	125	78.6		~180			
AMNH 11857	165	138	83.6			178		
F:AM 50329	168	129	76.8		193	172	89.1	
CM 492	185	135	73.0		201	179	89.0	
FMNH P12021		140			197	178	90.3	
FMNH P12138	~155	~119	76.7	54.4[c]	~175	156	89.1	56.6
FMNH UM746	~170	135	79.4			~180		
F:AM 63343		131		47	187			
PU 11423					197			
PU 12588	163							
Daphoenus hartshornianus								
F:AM 76529					152	~142	93.4	52.3
FMNH UM488	~112	~93	83.0		143	135	94.4	
Daphoenus sp. *(Chadronian)*								
CM 951					142	137	96.4	
FMNH PM8694	136	109	80.1					
UNSM 26171	132	108	81.8		~158	149	94.3	
UNSM 48498	134	110	82.0					
Daphoenodon superbus								
CM 1589	210	182	86.7		230	205	89.1	
AMPHICYONINAE								
Ysengrinia americana								
CM 2400	300							
UNSM 44606	287							
F:AM 54147	270	~241	89.3					
USNM 186993					351	~280	79.8	
UNSM 44600		260						
UNSM 44601		250						
UNSM 44691		252						
UNSM 44624					364			
UNSM 44690					353			
UNSM 44620						287		

TABLE 11
(Continued)

Mus. No.	Humerus	Radius	R/H	MC4	Femur	Tibia	T/F	MT4
UNSM 44621						297		
UNSM 44622						287		
UNSM 44623						288		
Cynelos lemanensis[d]	220	197	89.5		282	240	85.1	
Amphicyon major[e]	294	239	81.3		330	258	78.2	

R/H = humeroradial ratio, T/F = femorotibial ratio (Davis, 1964), MC, MT = metacarpal, metatarsal.
[a]All limb bone lengths in mm.
[b]Calculated from ulna length.
[c]Metacarpal 3.
[d]From Ginsburg (1977).
[e]From Bergounioux and Crouzel (1973).
[juv]Juvenile individual (Schlain, 1980).

survive (table 11). A complete set of associated metacarpals is known only for *T. ferox* (table 8), preserved in a strongly silica-cemented, recalcitrant matrix in which anatomical detail is obscured. The metatarsals fare better: a complete or nearly complete set is known for *T. ferox*, *M. obtusidens*, and *D. oryktes*. This is fortunate since the reduction

TABLE 12
Limb Proportions of Living Ursids, Felids, and Canids Relative to Oligocene-Miocene Amphicyonid Carnivorans, *Hyaenodon* and *Dinictis*

Family	Species[a] (N)	Humeroradial ratio	Femorotibial ratio
URSIDAE	*Ursus arctos* (7)	79.0–83.1	67.9–73.9
	Ursus americanus (3)	78.3–84.4	71.4–75.9
	Thalarctos maritimus (2)	84.4–86.3	73.9–74.4
FELIDAE	*Panthera tigris* (9)	80.7–86.4	83.4–87.6
	Panthera leo (11)	90.0–94.0	83.7–89.3
CANIDAE	*Canis lupus* (4)	97.2–101.9	96.5–100.9
	Canis latrans (3)	104.4[b]	99.6[b]
	Chrysocyon brachyurus (2)	108.1[b]	107.8[b]
AMPHICYONIDAE			
DAPHOENINAE	*Daphoenus vetus* (8)	73.0–83.8	89.0–90.3[c]
	Daphoenus hartshornianus (1, 2)	83.0	93.4–94.4
	Daphoenus (Chadronian) (3)	80.1–82.0	94.3–96.4[c]
	Daphoenodon superbus (1)	86.7	89.1
AMPHICYONINAE	*Ysengrinia americana*	87.1–90.6[d]	78.8–84.1[e]
	Cynelos lemanensis (1)	89.5	85.1
TEMNOCYONINAE	*Temnocyon altigenis* (1)	83.0	
	Temnocyon ferox (1)	90.3	91.0
	Mammacyon obtusidens (1)	94.5	
	Mammacyon ferocior (1)	91.9	96.4
	Delotrochanter oryktes (1)	95.4	92.7
HYAENODONTIDAE	*Hyaenodon horridus* (1)	71.6	86.0
NIMRAVIDAE	*Dinictis* sp. (1)	81.3	86.3

[a]Ratios for living species calculated from data in Hunt (2002a: table 2).
[b]Mean, from Davis, 1964: 35.
[c]Femorotibial ratio, *D. vetus*, N = 4; Chadronian *Daphoenus*, N = 2.
[d]Range of values based on a humerus and three radii from the same quarry.
[e]Range of values based on two femora and four tibiae from the same quarry — most probable ratio falls between 81.3 and 81.6.

of the outermost metatarsals and digits can be identified in all of these species, supplying critical information on the evolution of the hind foot. Phalanges directly associated with the corresponding metapodials are only preserved in the fore- and hind foot of *T. ferox*; yet because its limbs are so like those of species in the other two genera, one can infer the presence of proportionately similar phalanges.

Limb Proportions

Limb proportions of temnocyonines are compared with those of living ursids, felids, and canids in table 12. Proportions of some daphoenine and amphicyonine beardogs are also included, with *Daphoenus vetus* representing the inferred plesiomorphic limb skeleton for North American daphoenine amphicyonids. (For further comparison, table 12 includes a contemporary White River creodont, *Hyaenodon horridus*, and White River nimravid cat, *Dinictis* sp., both with limb ratios indicating lack of limb elongation.)

The more complete data from the forelimb is supplemented by the sparser hind limb measurements. Together they demonstrate the lengthening of the lower limb segments in temnocyonines. The evident correspondence to the limb proportions of living canids is striking, and exceeds the degree of elongation in living ursids, felids, and in other amphicyonids. The forelimb of the lion *Panthera leo* is similar in length to those of several temnocyonines but the lion hind limb is not quite as elongate.

The Logan Butte temnocyonine skeleton (*T. altigenis*, UCMP 9999) is the most anatomically primitive. Most limb bones are present but few are complete. Although only the humerus is intact, an estimate of forelimb length can be based on a radius and ulna lacking only their distal ends. If this estimate is correct, the forelimb has not yet lengthened to the extent evident in younger, larger temnocyonine species. *Temnocyon altigenis* from Logan Butte retains a plesiomorphic cranium and dentition little different from the North American amphicyonid *Daphoenus vetus*, and forelimb measurements of these two species also show similar, less elongated limb proportions. However, UCMP 9999 displays less angulation of its elbow joint than seen in *D. vetus*, suggesting that a more parasagittal excursion of the forelimb had been achieved in *T. altigenis* relative to *D. vetus*. The inference that forelimb elongation in temnocyonines occurs in parallel as each lineage evolves over time is based on the absence of elongation in the forelimb of the Logan Butte *Temnocyon* (UCMP 9999), which retains the most plesiomorphic dentiton and skull of the subfamily.

The oldest species of *Mammacyon* and *Delotrochanter* associated with postcrania already possess elongated limbs. Whether the earlier representatives of these genera were similarly proportioned is unknown; there is no reason why they could not have evolved from an ancestral species such as the Logan Butte *Temnocyon*.

Cursorial Adaptations in the Limb Osteology of Temnocyonines

Cursorial traits are particularly evident in the osteology of the forelimb and these approximate similar adaptations in the forelimb of the wolf (*Canis lupus*) and cheetah (*Acinonyx jubatus*). Plesiomorphic amphicyonid postcranial morphology is represented by the Oligocene *Daphoenus vetus* Leidy (Hatcher, 1902b; Scott and Jepsen, 1936). The following comparisons of the smaller temnocyonine species are with *D. vetus*, while the large temnocyonines are compared with *Daphoenodon superbus* (Peterson, 1910), whose skeleton can be considered an essentially unmodified, scaled-up version of that of *D. vetus*.

Forelimb

Scapula: *Delotrochanter oryktes* (ACM 4804) preserves the only relatively complete scapula known for temnocyonines (fig. 57). The scapula of ACM 4804 is most similar in form to those of other contemporary amphicyonids (e.g., *Daphoenodon superbus*, *Borocyon niobrarensis*; Hunt, 2009: fig. 20A). Among the living Carnivora its shape approaches the scapular form of felids. Schlain (1980) established the presence of a postscapular fossa for the subscapularis muscle in this species, a feature typical of amphicyonids. The supraspinous fossa occupies pro-

portionately more surface area than the infraspinous fossa, and acromnion and metacromnion processes are present. Schlain (1980) noted the narrow glenoid cavity implying restriction of the movement of humerus on scapula to a more fore-aft path. The spinodeltoid, which flexes the shoulder, runs from the scapular spine to the deltoid crest of the humerus; this crest in temnocyonines is a low arcuate ridge that traverses the upper two-thirds of the diaphysis.

In *Temnocyon altigenis* (UCMP 9999) only the glenoid of the scapula survives. *Temnocyon ferox*, the only other species of this genus that is represented by most of the postcranial skeleton, also retains a glenoid remnant as does *Mammacyon ferocior* (F:AM 27562). The holotype of *Mammacyon* (*M. obtusidens*, ACM 34-41) preserves the glenoid and adjoining portion of the scapular blade including the scapular spine. The spine terminates anteriorly in a very small, blunt acromnion process (there is no metacromnion process), much less developed than even that of the wolf. This suggests a reduced acromiodeltoid muscle, a forelimb abductor less necessary in a cursor. In this respect the scapula of *M. obtusidens* differs from the more plesiomorphic scapula of *D. oryktes* with its prominent acromnion and metacromnion processes.

HUMERUS: The humerus is complete in *Temnocyon altigenis* (UCMP 9999) and already displays a more specialized distal anatomy than seen in *D. vetus* (fig. 51). While these two species have humeri of equal length, the distal humerus of UCMP 9999 is transversely narrower, shows reduction of the medial epicondyle, and possesses a deeper olecranon fossa for reception of the ulna. These traits accompany a close congruent registration of the humeroulnar articulation, effective in restricting the ulna to flexion-extension on the humerus when the lower limb is extended, and thus favoring a parasagittal trajectory for the lower forelimb. A rotational torque at the elbow is resisted by contact of a facet on the lateral face of the anconeal process of the ulna with the lateral margin of the olecranon fossa of the humerus, assisted by the tight contact of the ulna's coronoid process with the humeral trochlea. This type of humero-ulnar joint registration, which occurs in temnocyonines, was previously noted by Jenkins (1973) who observed that reduction of the medial epicondyle and its associated flexor musculature decreases torque at the elbow. These features are a prelude to a more erect forelimb stance, evident in both the Logan Butte *T. altigenis* and *T. ferox*.

Both *Mammacyon obtusidens* and *M. ferocior* preserve the humerus, damaged in the former species, nearly complete in the latter. In both species the form of the bone is identical except for greater size in *M. ferocior*. As in *Temnocyon*, the distal humerus is specialized for fore-aft excursion of ulna on humerus, as evidenced by a narrow transverse distal width, reduction of the medial epicondyle, and a deep symmetrical olecranon fossa (fig. 52). All temnocyonine humeri exhibit a more rounded capitulum and deeply grooved trochlea than seen in those of *Daphoenus vetus* and *D. superbus*, a condition seemingly related to the narrow distal articular width of this bone. This differs from the more cylinder-like, wider articular surface of *Daphoenodon superbus* and *D. vetus*, which lacks the rounded capitulum.

The humerus of *Delotrochanter oryktes* (ACM 4804), ~22 cm in length, is much the same size as the humerus of *M. obtusidens*, and is nearly as large as the humerus of *M. ferocior* (~24.5 cm). The humerus is straight-shafted, a trait common to all larger temnocyonines (figs. 53–55); the bone has a slimmer profile in lateral view due to the reduction of the plesiomorphic amphicyonid deltopectoral crest and its restriction to the proximal humerus. The proximal placement and reduction of this crest also occurs in *Canis lupus*. The distal anatomy of the humerus is identical to that seen in other temnocyonines (fig. 52), indicating a similar upright stance and fore-aft excursion of ulna on humerus.

RADIOULNA: The radius is known in species of *Temnocyon*, *Mammacyon*, and *Delotrochanter*. In the Logan Butte *Temnocyon altigenis* both radii are present but lack their distal ends. In *Temnocyon ferox* the forelimb preserves a fully articulated radius, ulna, and humerus (fig. 53) but these bones are so fragmented that details of the articular surfaces are obscure. The forelimb does not

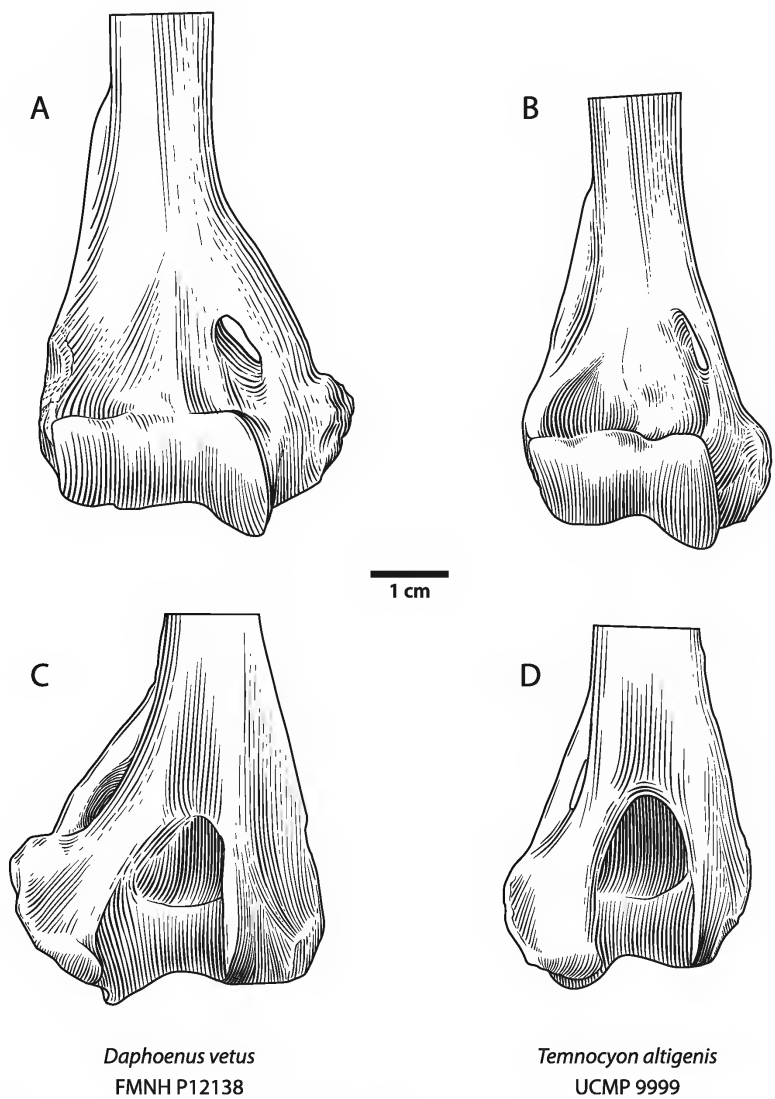


Fig. 51. Comparison of the distal humerus of a stem daphoenine (**A, C**: *Daphoenus vetus*) and a plesiomorphic temnocyonine (**B, D**: *Temnocyon altigenis*). The daphoenine amphicyonid humerus is distally broad for developed flexors arising from the medial condyle and has an asymmetric olecranon fossa indicating an everted elbow. Temnocyonines have evolved the narrow distal humerus of cursorial carnivores with reduced medial condyle and symmetric olecranon fossa corresponding to an elbow with a more fore-aft alignment.

show significant elongation in *T. altigenis*, however with the younger *T. ferox* some elongation of the forelimb has taken place (table 11). The articulated forelimb of *T. ferox* makes possible a reliable estimate of limb proportions in this carnivore.

Forelimb proportions were also calculated from an associated humerus, radius, and ulna for *T. altigenis*, *T. ferox*, *M. obtusidens*, and *D. oryktes* and compared with other carnivorans (table 12). For *M. ferocior* where no radius was found, an associated humerus and ulna determine the length of the radius. The forelimb proportions for *Mammacyon* and *Delotrochanter* show that elongation of the radioulna contributes to lengthening of the limb.

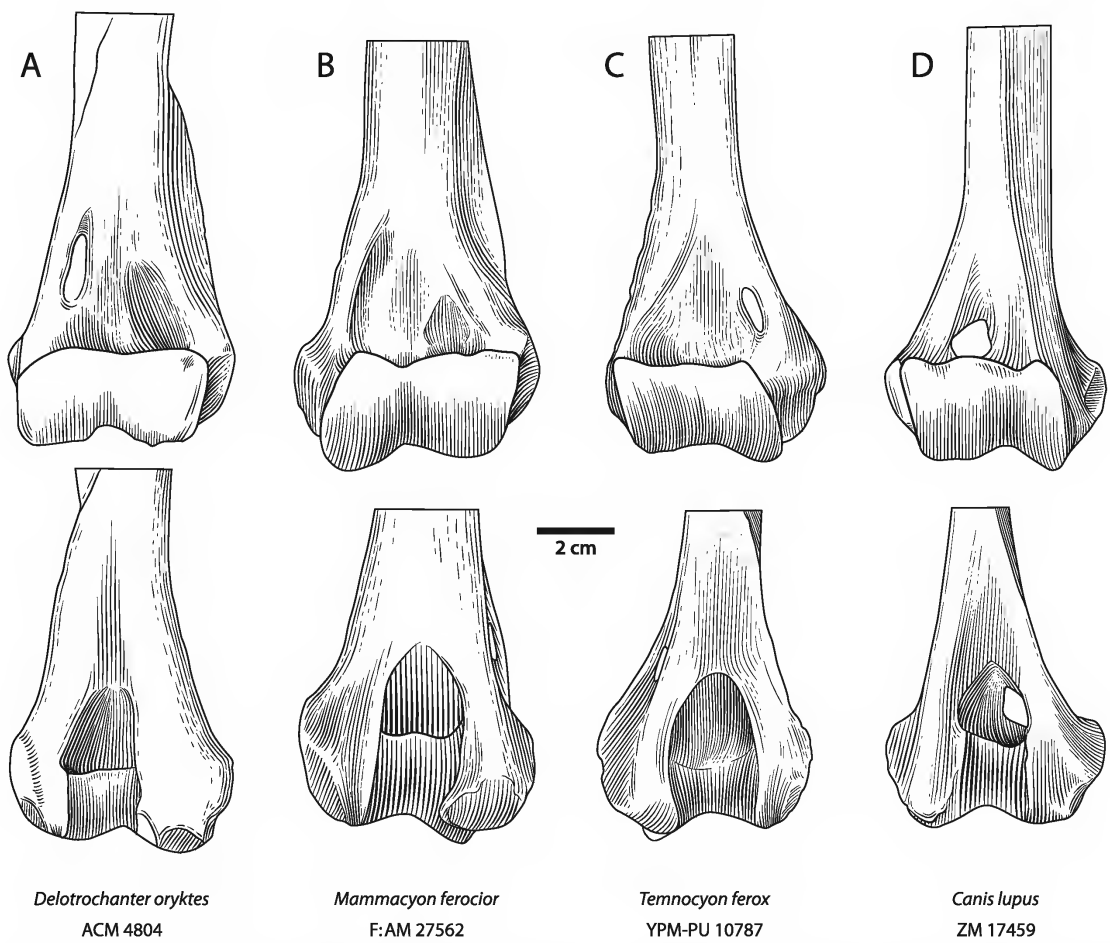


Fig. 52. All temnocyonines have developed a narrow distal humerus (with reduced medial condyle, symmetric olecranon fossa) in which the forelimb shows little or no eversion at the elbow as also seen in the wolf. These forelimbs adopt an erect digitigrade stance. Upper row, anterior view; lower row, posterior view. **A,** *Delotrochanter oryktes*; **B,** *Mammacyon ferocior*; **C,** *Temnocyon ferox*; **D,** *Canis lupus*. A, B: left humerus; C, D: right humerus.

Although no radius was collected with *M. ferocior*, its humerus and ulna (fig. 54) are identical to those of *M. obtusidens* and so a similar radius can be inferred; these two species differ only in the larger size of *M. ferocior*. Here the narrow distal humerus, best preserved in *M. ferocior*, confines the ulna to fore-aft flexion and extension. When the radioulna is extended on the humerus, the movement of the lower limb is plainly fore-aft in direct parasagittal alignment with the humerus. The rounded capitulum and grooved trochlea of the distal humerus are congruent and register exactly with the circular, concave radial head and the semilunar notch and coronoid process of the ulna—these joint surfaces correspond closely in form to those of the wolf (fig. 54). However the radial head is not as limited in its rotation in the radial notch of the ulna as it is in the wolf, and the humeral trochlea not quite as narrow. Similarly, the bicipital tuberosity of the radius in *Mammacyon* remains better developed than in the wolf, suggesting that some ability to pronate/supinate the lower limb and forepaw was still retained.

Delotrochanter oryktes (ACM 4804) is represented by a humerus, radius, and ulna (fig. 55) that show anatomical modifications like those of *Mammacyon*. In particular, the

Fig. 53. Articulated right forelimb of the holotype of *Temnocyon ferox* (YPM-PU 10787), John Day Formation, Oregon. The forefoot shows elongation of the paraxonic metacarpals 3, 4, and their digits, with reduction of metacarpals 1, 2, and 5 (metacarpal 5 is hidden from view). A partial femur (fe) and tibia (ti) of an oreodont were entombed with the beardog. Abbreviations: sc, scapula; hu, humerus, ul, ulna; ra, radius; cp, carpus; nos. 1–4, metacarpals; pr, proximal phalanx; ip, intermediate phalanx.

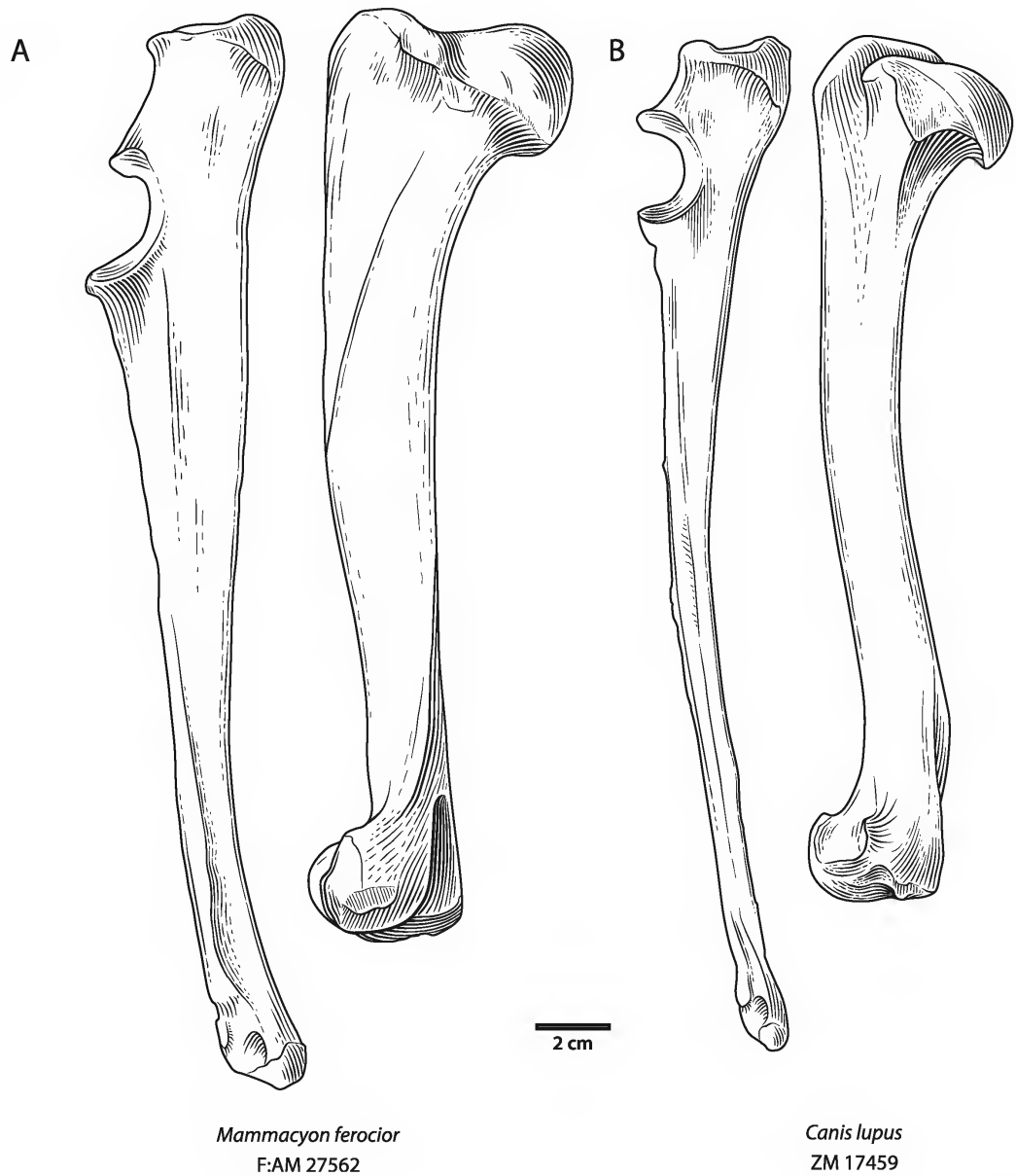


Fig. 54. Associated humerus and ulna of (**A**) *Mammacyon ferocior* and (**B**) *Canis lupus* showing elongation of the ulna (and radius) and pronounced reduction of the distal ulna in these cursors.

proximal ulna is a mediolaterally compressed, thin bone as in the wolf, and the semilunar notch is proximodistally divided by a low ridge, which fits into the groove of the trochlea of the humerus, aiding in humero-ulnar registration in wolf and *D. oryktes*. These features are not found in the less cursorially patterned elbow joint of *Daphoenodon superbus*.

Moreover, the head of the radius has a precise articulation with the radial notch of the ulna in *Delotrochanter* and *Mammacyon* that differs from this articulation in the wolf: in the wolf when the radial head is placed in the radial notch, the radial head is positioned somewhat in front of the ulna. However in *Mammacyon* and *Delotrochanter*, when the radial head is placed in the laterally facing

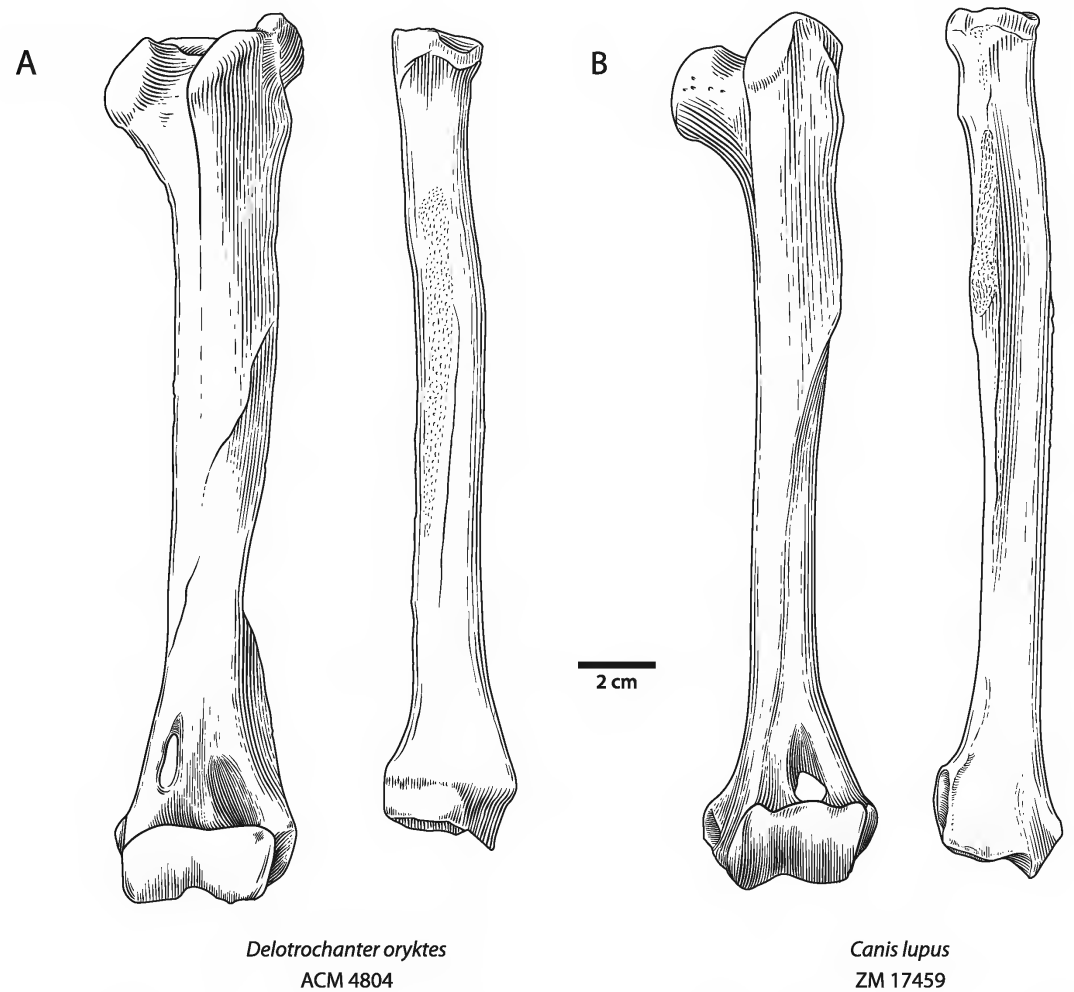


Fig. 55. Humerus and radius of (**A**) *Delotrochanter oryktes* and (**B**) *Canis lupus*. Anatomy of the *D. oryktes* forelimb and elongation of the radius and ulna are similar to these features in the wolf. Left humeri, anterior view; left radii, posterior view.

notch, the radial head is situated lateral to the ulna, which corresponds to the placement of the capitulum of the humerus directly lateral to the trochlea. This more side-by-side articular relationship of the proximal radius and ulna seems exclusive to temnocyonines. But most important for fore-aft excursion of the limb is that the shaft of the radius in these temnocyonines aligns more in parallel to the shaft of the ulna, as in the wolf. In *D. oryktes* and *M. ferocior*, the radius lies in close apposition to the ulna, much more so than in *Daphoenodon superbus* where the shaft of the radius is aligned at a greater angle to the shaft of the ulna.

Furthermore, in temnocyonines the extent of the articular facet on the radial head suggests that rotation of the radius on the ulna was limited. In the wolf a limit to the amount of rotation of the radius in the radial notch of the ulna is evident from the shape of a well-defined articular facet on the radial head that incorporates a bony stop on its lateral edge. The articular facet ends sharply where it articulates with the lateral extension of the coronoid process of the ulna, which has been reduced to a thin flange in both temnocyonines and the wolf. The even greater reduction of this flange in temnocyonines seems to be due to the more lateral

placement of the radial head relative to the ulna in these beardogs.

In temnocyonines where the distal ulna is preserved, the distal articulation for the carpal cuneiform is present, but the articular process contacting the radius is much reduced. This parallels the condition in cursorial wolves and coyotes, in which rotation of radius on ulna is restricted.

FOREFOOT (CARPUS, METACARPUS, PHALANGES): Bones of the forefoot rarely survive among temnocyonines. In *T. altigenis* from Logan Butte no forefoot elements are known. The forelimb of *Temnocyon ferox* (YPM-PU 10787), however, includes a partially articulated paraxonic forefoot with carpals, metacarpals, and phalanges (fig. 53) that demonstrates the relative proportions of these elements. Metacarpals 1 to 5 of *T. ferox* are all slightly elongated relative to those of *Daphoenodon superbus*, and the paraxonic metacarpals 3–4 are more robust as well as longer. In *T. ferox* the trapezium, first metacarpal, and its phalanx indicate a much reduced, thin first digit in the forefoot. However, this degree of reduction of the first digit does not equal the more extreme state seen in the wolf. Although the metacarpals of *T. ferox* are not tightly appressed as in the wolf, they are in closer contact than in *Daphoenodon*.

In the forefoot of *T. ferox* the proximal phalanges of digits 3–4 are long (both ~31 mm), those of digits 2 and 5 shorter (~27–29 mm), and that of metacarpal 1 reduced (length, 21.8 mm). Intermediate phalanges of digits 3–4 are short (length, ~19 mm). Only in digit 4 has the ungual been preserved; it is short (length, ~13 mm) and rather blunt. The phalanges of paraxonic digits 3–4 are more robust than those of *D. superbus*. If *T. ferox* is representative of the subfamily, temnocyonines lack the extreme elongation of the proximal and intermediate phalanges seen in the wolf.

The scapholunar, unciform and trapezium of *Temnocyon ferox* are proportionately smaller than those of *D. superbus* and are most like those of the wolf (a small carpal cuneiform is obscured by sediment). Thus the carpus is transversely narrow in order to accommodate a distally narrow radius and ulna, as in the wolf.

TABLE 13
Measurements (in mm) of the Unciform in *Temnocyon*, *Delotrochanter*, *Daphoenodon*, and the Live Oak Carnivore

Taxon	Greatest height	Greatest width[a]
Temnocyon ferox		
(YPM-PU 10787)	14.0	14.6
Live Oak (TRO 661)	18.0	18.5
Delotrochanter oryktes		
(ACM 4804)	19.2	20.0
Daphoenodon superbus		
(CM 1589)	16.3	12.5

[a]Width measured across the anterior face of the unciform.

However, the carpus lacks some anatomical features evident in wolves. The unciform serves as a case in point. The temnocyonine unciform from the Live Oak site in Florida (table 13) confirms that this bone was low and broad, much different in form from the tall, narrow unciforms seen in living ursids and felids. The Live Oak unciform shows a marked similarity to that of *Canis lupus* (the wolf is 23% smaller) except that a stop facet on the wolf unciform for the scapholunar is absent in the Live Oak beardog (Hunt, 2009: fig. 25, *Canis lupus*, #3). In both temnocyonine and wolf the unciform articulates with metacarpals 4–5, but in the wolf the carpal cuneiform, in close contact with the unciform, bends down around the unciform and articulates by a defined concave facet with the head of metacarpal 5. There is no evidence of such a specialized carpal cuneiform in temnocyonines, and it is not present in the articulated carpus of *Temnocyon ferox* or in *Delotrochanter oryktes* (ACM 4804). The canine carpal cuneiform strengthens the carpal-metacarpal joint where it extends outward in the wrist between the fifth metacarpal and unciform. In the wolf, the fifth metacarpal is a large bone but it is much reduced in *Temnocyon ferox* and *Delotrochanter oryktes*.

The few metacarpals of *Delotrochanter* and *Mammacyon* that are known (table 8) conform anatomically to those of *T. ferox* and indicate elongation of the paraxonic forefoot (fig. 56). The considerable length of paraxonic metacarpals 3–4, and the shorter metacapal 5 evident in *D. oryktes* (UNSM

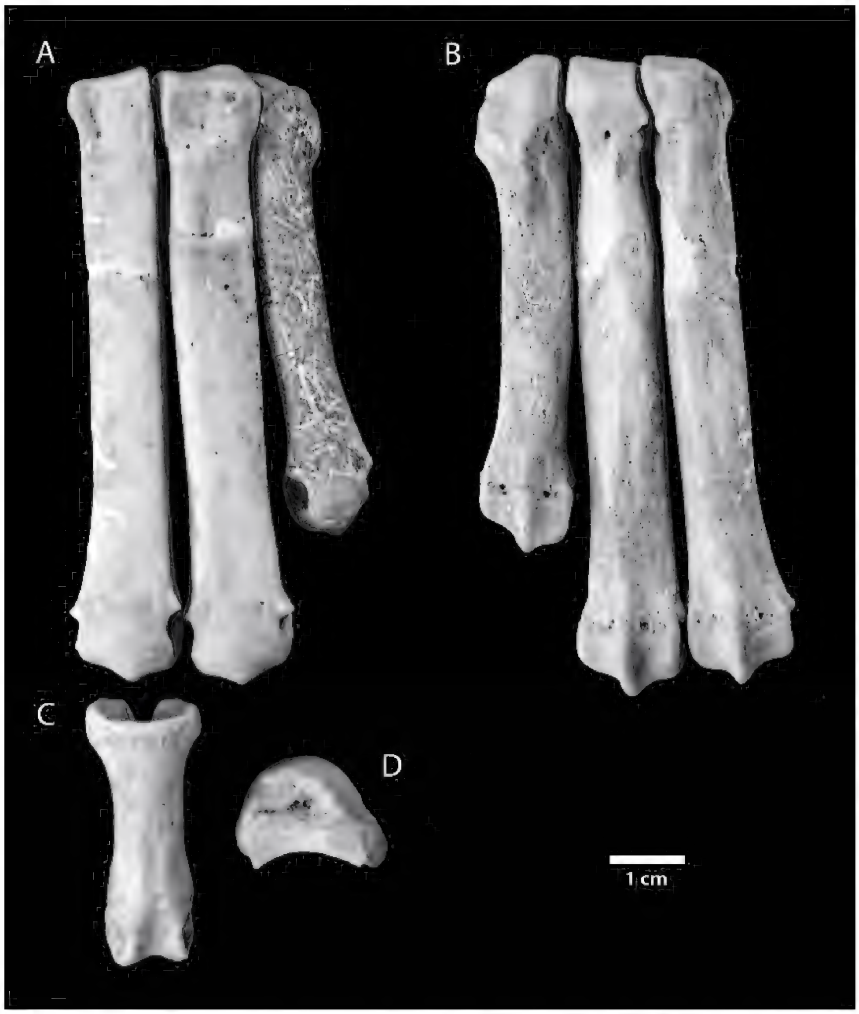


Fig. 56. Forefoot of *Delotrochanter oryktes* (UNSM 48700), from carnivore den, Beardog Hill, Agate Fossil Beds National Monument, Sioux Co., Nebraska. Metacarpals 3, 4, 5 (**A,** anterior view; **B,** posterior view); **C,** proximal phalanx of paraxonic digit of forefoot; **D,** magnum.

47800), together with metacarpals 2 and 5 in ACM 4804, show that the flanking metacarpals 2 and 5 were of similar length and were more reduced than those of the wolf, in which a robust metacarpal 5 plays a more prominent role. Only ACM 4804 preserves metacarpal 1, a small, thin, elongate bone (length, 37–38 mm), not as reduced as in the wolf.

Hind Limb

Innominate: The pelvis with sacrum in direct articulation survives in *Temnocyon ferox* and a damaged innominate is present in *Delotrochanter oryktes*, however a complete pelvis is not preserved in other temnocyonines. Only a partial innominate of the Logan Butte *T. altigenis* and fragments of the innominate of *M. ferocior* are known; these do not differ from the innominates of *T. ferox* and *Daphoenodon superbus* except in size. The innominate of *Delotrochanter oryktes* (ACM 4804) lacks only the terminus of the ischium and shares the same form and proportions as in *T. ferox* (fig. 57).

During excavation of the carnivore dens at Agate National Monument in 1985, we

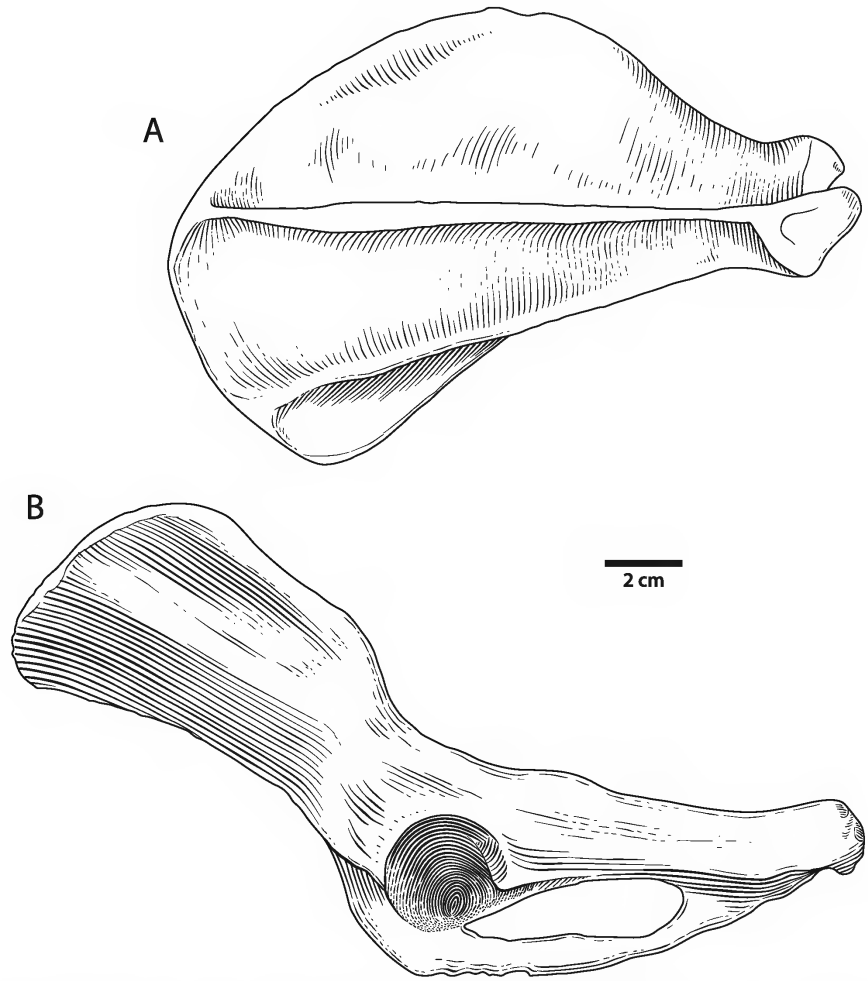


Fig. 57. Scapula (**A**) and innominate (**B**) of *Delotrochanter oryktes* (ACM 4804, ischium restored in part). The temnocyonine scapula did not often survive but in this species it is most similar to the plesiomorphic scapulae of *Daphoenus* and *Daphoenodon superbus*. The innominate, also known in *Daphoenodon superbus* and in *Temnocyon ferox*, has an extended ischium that presumably provided a mechanical advantage for the action of hamstring muscles.

recovered a nearly complete innominate of *D. superbus* with ischium and pubis intact. The most striking difference in the pelvis of *Daphoenodon* and the temnocyonines relative to that of a wolf is the much longer ischial region relative to the ilium—the postacetabular distance in the wolf is ~68% of the preacetabular distance, whereas in *T. ferox* this is 84%, in *D. oryktes* 83%–87%, and in *D. superbus* 98%. In the wolf the posterior ischium is rotated outward, presumably to increase the mechanical advantage of the hamstring muscles. This ischial eversion is absent in temnocyonines, but the simple lengthening of the ischium may have provided a similar mechanical advantage.

The temnocyonine sacrum also differs from that of the wolf in its narrow, elongate shape compared to the short, broad sacrum of *Canis lupus*. These sacra all include three fused vertebrae but the transverse processes are more elongated and developed in the wolf, giving the sacrum its broader appearance. In the Logan Butte *Temnocyon altigenis*, *T. ferox*, and *Mammacyon ferocior*, and in *Daphoenodon superbus*, the width of the sacrum (measured at the 2nd sacral vertebra) is 44–46% of the length but

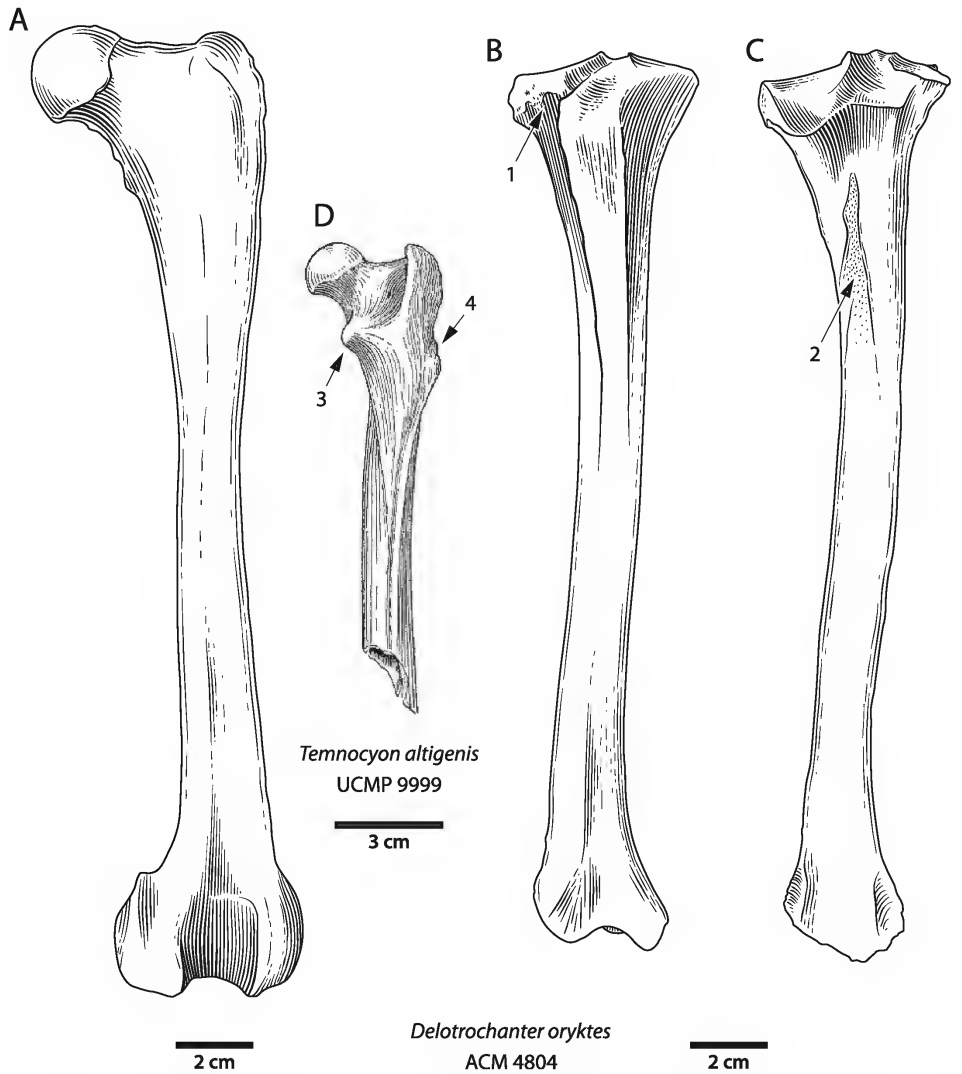


Fig. 58. Femur and tibiae of *Delotrochanter oryktes*, *Stenomylus* Quarry, Harrison Formation, Agate Fossil Beds National Monument, Nebraska. The long slender femur (**A**) and tibiae (**B,** right; **C,** left) are similar in proportion and form to those of the wolf whose tibia is ~8% longer. An arrow (**1**) marks the *sulcus muscularis* in **B**. Muscle scars (**2,** stippled) on the posterior tibia (**C**) indicate proximally situated posterior tibial and long digital flexor muscles. The femur (**D**) of *Temnocyon altigenis*, the smallest and most primitive temnocyonine, retains a lesser trochanter (**3**), gluteal flange, and third trochanter (**4**). A, B in anterior view; C, D, posterior view.

in the wolf this value is 88%. Nonetheless, the articular surface of the ilium with the sacrum is of similar proportions in all these carnivores.

Femur-Tibia: An associated femur and tibia occur in *Temnocyon ferox*, *Mammacyon ferocior*, and *Delotrochanter oryktes* (fig. 58). Thus, hind limb proportions can be estimated for representatives of the three principal temnocyonine genera (tables 11–12). In these three species the femorotibial proportion varies from 91% to 96%, approaching the ratio found in wolves (~96%–101%). Lower indices of 67%–76% in ursids, and 83%–89% in felids, reflect the shorter tibiae in these living carnivores. The indices for the daphoenine amphicyonids (89%–96%), while similar to those of temnocyonines (91%–96%), are

lower for the large, terrestrial *Daphoenus vetus* (~89%–90%) and higher for the small scansorial *D. hartshornianus* and the Chadronian forms (~93%–96%). Despite the proportionately longer hind limbs in these latter two groups, their forelimbs remain quite short (80%–83%, ratio R/H, table 11) and show that *D. hartshornianus* and the Chadronian daphoenines differ from the temnocyonines who evolved longer forelimbs (~90%–95%, ratio R/H) relative to the hind limb. The earliest temnocyonines probably retained short, plesiomorphic forelimb proportions, since the forelimb of the Logan Butte *Temnocyon altigenis* lacks conspicuous elongation.

The temnocyonine femorotibial ratios suggest that other morphological correlates of an elongate cursorial hind limb might be present, and such is the case. For both *Delotrochanter oryktes* and *Mammacon ferocior* a prominent groove, the *sulcus muscularis* for the tendon of the long digital extensor, indents the lateral margin of the tibial platform immediately anterior to the lateral condyle (fig. 58B). From its origin on the femur, the tendon travels distad to extend the digits and participate in tarsal dorsiflexion. Although common in artiodactyls and perissodactyls, the sulcus is well developed among living Carnivora only in canine canids and the cheetah, and is not found in other arctoid carnivorans (ursids, procyonids, mustelids) or in *Daphoenus* and *Daphoenodon*. The sulcus is not quite as deep in *Mammacyon ferocior* and *Delotrochanter oryktes* as in the wolf. The tibia of *T. ferox* does not have a *sulcus muscularis*; thus it may have been acquired independently in *Mammacyon* and *Delotrochanter* (the proximal tibia was not recovered in *T. altigenis*). Except for size, the tibiae of *Temnocyon ferox*, *Mammacyon ferocior*, and *Delotrochanter oryktes* correspond closely in form and anatomy; the diaphyses are somewhat more robust when compared to the more slender tibia of the wolf.

Mammacyon ferocior and *Delotrochanter orkytes* also compare closely with the wolf in the pattern of muscle scars on the posterior surface of the tibia (fig 58C). The pattern indicates that the posterior tibial (PT) and long digital flexor (FDL) muscles have been reduced, and are proximally situated, a condition seen in the wolf (Evans, 1993) where the hind foot is specialized for fore-aft movement on level ground. The large temnocyonines, *Canis lupus*, and the cheetah *Acinonyx* exhibit this PT-FDL reduction more so than the large, living felids and ursids. For *M. ferocior*, tibial length (265 mm) relative to the width of the PT-FDL scar (~5 mm) corresponds to the values found for the wolf and cheetah (Hunt, 2009: fig. 30). However, temnocyonines differ from the wolf in the shallower registration of the astragular trochlea in the distal tibia, which is like that of the cheetah; deeper penetration of the astragalus in the wolf creates a more tightly registered joint.

Delotrochanter oryktes (ACM 4804) preserves both femora, described by Schlain (1980), who noted their resemblance to those of *Canis*. The femur is long, slender, slightly curved in the sagittal plane as in the wolf, but with the femoral head and neck almost at a right angle to the diaphysis (fig. 58A). This orientation of femoral head, neck, and diaphysis is typical of most amphicyonids and contributes to the adduction of the limb. The distal femur is transversely narrow and the condyles extend posteriorly as in the large living canids. In all these features the femur of *D. oryktes* is nearly identical to the femur of the cursorial daphoenine amphicyonid *Borocyon robustum* (Hunt, 2009).

The width of the femur across the distal condyles is narrow relative to femoral length in cursorial carnivores, and is similar among temnocyonines and the wolf, between 16% and 18% (table 14). However, the width of the groove for the patella relative to condylar width differs, for in temnocyonines the groove is from 41% to 46.5% of condylar width and in the wolf only 28%, indicating a narrower patellar groove in *Canis lupus*.

The femur of *Temnocyon altigenis* from Logan Butte (fig. 58D) can be articulated with the corresponding innominate to estimate the alignment of the hind limb in that species. Here the femur appears to be abducted ~20°–25° from the vertical, whereas abduction of 10° has been reported as the characteristic posture of living canids (Jenkins and Camzine, 1977). In *T. altigenis* the pit (fovea capitis) for the femoral ligament on the femoral head is situated as

TABLE 14
Dimensions of Femoral Condyles and Patellar Groove Relative to Femoral Length in Temnocyonines and *Canis lupus* (in mm)

Taxon	CW[a]	FL[b]	CW/FL	WPG[c]	WPG/CW (%)
Temnocyon ferox	40.0	244	16.4%	16.4	41.0
Mammacyon ferocior	47.0	~275	17.1%	19.7	41.9
Delotrochanter oryktes	40.8	246	16.6%	19.0	46.5
Canis lupus	44.5	252	17.6%	12.5	28.0

[a]CW= transverse width across distal condyles.
[b]FL = greatest femoral length.
[c]WPG = width of patellar groove (or patellar width as proxy).

in the larger canids (*Canis lupus*, *Lycaon pictus*) measured by Jenkins and Camazine (1977: fig. 9) and does not adopt the more extreme position found in living ursids and procyonids. In *Temnocyon ferox*, *Mammacyon ferocior*, and *Delotrochanter oryktes* the fovea capitis is similar in its placement to the fovea of *T. altigenis*.

The extent and orientation of the articular surface of the femoral head as it registers in the acetabulum provides a measure of the range of motion of the femur. Jenkins and Camazine (1977) measured the angle formed by a line drawn along the margin of the anterior articular surface of the femoral head and the femoral diaphysis; this angle in *D. oryktes* and *M. ferocior* (~38°–40°) was similar to that of *Canis lupus* (~40°), which suggests that the temnocyonines hold the femur in a more abducted position than in small cats and foxes, but with much less abduction than in procyonids and the large living ursids.

Jenkins and Camazine (1977) observed only modest extension of the articular surface of the femoral head in the proximal and posterior directions in canids. In *T. altigenis* and *T. ferox* the articular surface of the femoral head approximates that seen in the wolf, and does not extend downward on the posterior surface as in carnivores such as procyonids and ursids with greater femoral excursion employed in actions such as climbing, where a greater range of abduction-adduction occurs. In *D. oryktes* and apparently in *M. ferocior* the extent of the articular surface on the posterior femoral head does somewhat exceed that of the wolf so that the excursion of the femoral head in the acetabulum may have been more similar to the conformation in the large living cats (Schlain, 1980).

The femur of *T. altigenis* is unusual in having a gluteal ridge distal to the greater trochanter, forming a pronounced flange that continues along the outer diaphysis (Merriam, 1906: 27). The flange thickens to form a third trochanter ~35 mm distal to the greater trochanter for insertion of the superficial gluteal (fig. 58D, #4). This gluteal flange also occurs in *Daphoenus* and in archaic carnivores such as the mesonychid *Pachyaena ossifraga* (O'Leary and Rose, 1995) and the miacid *Miacis petilus* (Heinrich and Rose, 1995). The presence of the gluteal flange, large third trochanter, and prominent lesser trochanter suggests retention of some mediolateral mobility in the hip joint of *T. altigenis* indicative of more abduction-adduction than found in small living canids. This is also supported by the prominent knoblike lesser trochanter in *T. altigenis* (fig. 58D, #3) that projects posteromedially as in terrestrial small carnivorans in which some abduction and lateral femoral rotation occur.

TARSUS: The astragalus and calcaneum in temnocyonines, together with rare distal tarsals in *Temnocyon altigenis, T. ferox*, *Mammacyon ferocior*, and *Delotrochanter oryktes*, demonstrate a modified daphoenine tarsal pattern evolving toward a hind foot similar to the canine type, adapted for fore-aft flexion and extension and an erect digitigrade stance.

The form of astragalus and calcaneum approach that of living large canids, most closely in *T. ferox*, *M. ferocior*, and *D. oryktes*. The temnocyonine calcaneum is

both proximally and distally narrow relative to *Daphoenus*, *Daphoenodon superbus*, and amphicyonines (fig. 59, table 15). Calcaneal width at the sustentaculum is ~35%–42% of calcaneal length in temnocyonines, but in short-limbed daphoenines this measures from 46.6% to 52.1% (fig. 60). This reduction in width is already evident in *Temnocyon altigenis*. Also in temnocyonines, the sustentaculum appears proximally elevated because the distal calcaneum is lengthened below the sustentaculum, and its posterior surface becomes deeply grooved for the deep digital flexor (flexor digitorum profundus), active during the stance phase in dogs (Evans, 1993). A calcaneum of this type occurs in the wolf and is also common to living felids whose proximal tarsals are similarly lengthened distad contributing to hind foot elongation.

The temnocyonine astragalus (table 16) shows three derived features that correspond to the form of the calcaneum. The distal process for articulation with the navicular is no longer tranversely aligned as in *Daphoenus vetus* and *Daphoenodon superbus* but has shifted to a more angled alignment (a long axis directed anterolaterad to posteromesad) beneath the trochlea. This type of astragalus is known in *Temnocyon altigenis, T. ferox*, *Mammacyon obtusidens*, *M. ferocior*, and *Delotrochanter oryktes*. These temnocyonines also share a derived placement of the sustentacular facet situated proximally on the neck whereas in *D. superbus* and amphicyonines this facet extends far distad. Temnocyonines also possess a relatively narrow astragalar trochlea when compared to *Daphoenodon superbus* (table 16). By articulating the calcaneum and astragalus with the tibia in *T. ferox*, *M. ferocior*, and *D. oryktes*, the alignment of joint surfaces suggests a more erect hind foot stance as in large living cats and *Canis lupus*.

The complete articulated tarsus of *Temnocyon ferox* was illustrated by Eyerman (1896). The plesiomorphic tarsal pattern of daphoenines such as *Daphoenus vetus* and *Daphoenodon superbus* differs from the derived pattern evident in *Temnocyon ferox* (fig. 61), in which a mediolaterally narrow tarsus had evolved, paralleling the cursorial wolf. This derived state was also present in *Mammacyon* and *Delotrochanter*.

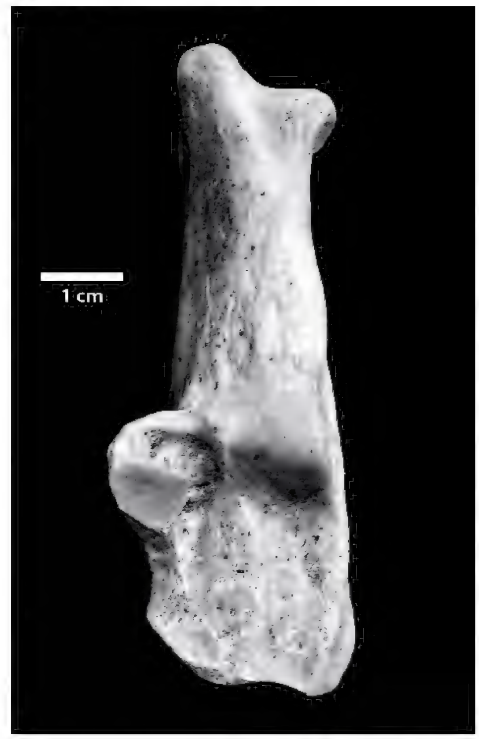


Fig. 59. Calcaneum of *Delotrochanter oryktes* (UNSM 47800), from temnocyonine carnivore den, Beardog Hill, Agate Fossil Beds National Monument, Sioux Co., Nebraska.

Distal tarsals of temnocyonines have survived in *M. ferocior* (F:AM 27562: associated navicular, cuboid, and ectocuneiform) and in *D. oryktes* (ACM 4804: navicular and ectocuneiform). In primitive daphoenines the cuboid shows the expected facets for the ectocuneiform and navicular but also retains a plesiomorphic contact with the astragalus, whereas in the wolf and temnocyonines this astragalar contact is lost (fig. 62). Furthermore, in temnocyonines where the articulations among calcaneum, astragalus, navicular, and cuboid can be determined from facets, the distal calcaneum contacts the navicular, but in *Daphoenus* and *Daphoenodon superbus* the astragalus excludes the navicular from contact with the calcaneum. The calcaneal facet on the navicular is well developed in *M. ferocior* and *D. oryktes* and appears to be present in *Temnocyon altigenis* and *T. ferox*.

In wolf, *Mammacyon*, and *Delotrochanter*, the cuboid and navicular are in close contact,

TABLE 15
Calcaneal Dimensions of Temnocyonine and Daphoenine Amphicyonids (in mm)

Mus. No.	Taxon	Calcaneal height (H)	Sustentacular width (SW)[a]	SW/H (%)
Temnocyoninae				
UCMP 9999	*Temnocyon altigenis*	48.6	20.6	42.4
YPM-PU 10787	*Temnocyon ferox*	60.9	23.8	39.0
F:AM 27562	*Mammacyon ferocior*	78.0	28.0	35.9
UNSM 47800	*Delotrochanter oryktes*	71.1	26.0	36.6
YPM-PU 24872	*Delotrochanter oryktes*	66.0	26.6	40.3
UF 16908	temnocyonine indet.	63.1	22.4	35.5
Daphoeninae				
FMNH P12138	*Daphoenus vetus*	43.6	22.7	52.1
CM 1589 Left	*Daphoenodon superbus*	58.7	28.9	49.2
CM 1589 Right	*Daphoenodon superbus*	59.2	28.4	48.0
CM 1589b[b]	*Daphoenodon superbus*	67.4	32.3	47.9
CM 1589b[b]	*Daphoenodon superbus*	64.6	31.3	48.5
CM 1589c	*Daphoenodon superbus*	63.7	29.7	46.6
CM 2199	*Daphoenodon superbus*	60.1	29.0	48.3
UNSM 72-90	*Daphoenodon superbus*	~64	30.7	48.0
UNSM 423-78	*Daphoenodon superbus*	~60	28.1	46.8
UNSM 99420	*Daphoenodon falkenbachi*	72.4	34.0	47.0

[a]Transverse width of the calcaneum measured at the level of the sustentaculum.
[b]Calcanea numbered CM1589b represent two different individuals.

and their articular surfaces for the proximal tarsals lie in an essentially horizontal plane; the cuboid surface is only slightly convex and the navicular modestly concave. As a result of this nearly coplanar articulation of the proximal tarsals (calcaneum-astragalus) with the cuboid and navicular, the motion possible at the intratarsal joint limits rotation around

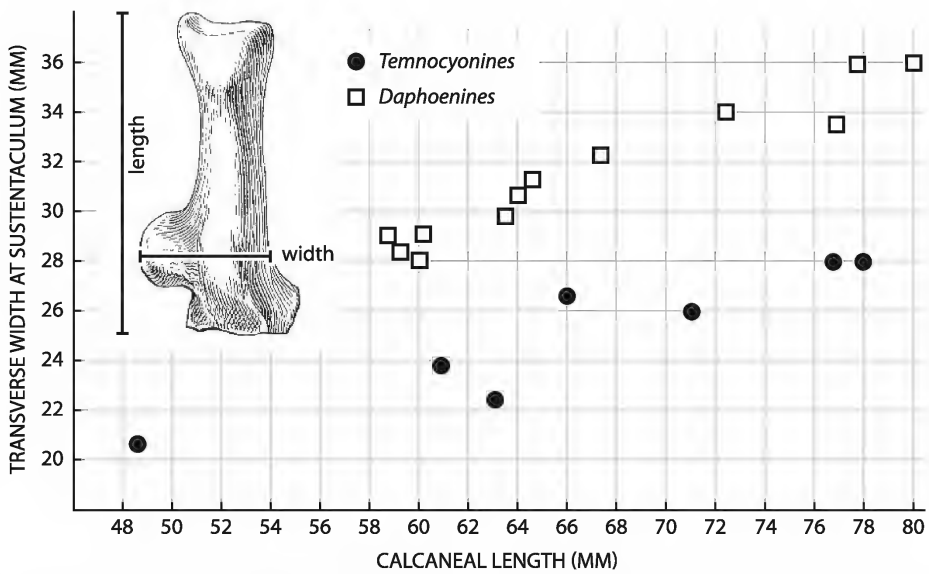


Fig. 60. Bivariate graph of calcaneal dimensions of temnocyonines relative to calcanea of daphoenine amphicyonids. A narrow, distally extended calcaneum similar to that of living digitigrade felids is characteristic of temnocyonines.

TABLE 16
Dimensions of the Astragalus in Temnocyonine and Daphoenine Amphicyonids (in mm)

Mus. No.	Taxon	Height (H)	Trochlear width (TW)	TW/H (%)
Temnocyoninae				
UCMP 9999	*Temnocyon altigenis*	—	~15	—
UCMP 1986	*Temnocyon altigenis*	25.9	14.0	54.0
YPM-PU 10787	*Temnocyon ferox*	33.8	~17	50.3
ACM 34-41	*Mammacyon obtusidens*	35.6	19.2	53.9
F:AM 27562	*Mammacyon ferocior*	42.1	23.5	55.8
ACM 4804	*Delotrochanter oryktes*	38.0	~21	55.3
Daphoeninae				
CM 1589 left	*Daphoenodon superbus*	35.3	20.2	57.2
CM 1589 right	*Daphoenodon superbus*	35.1	20.2	57.5
CM 1589c	*Daphoenodon superbus*	38.0	21.9	57.6
CM 2199	*Daphoenodon superbus*	39.4	22.7	57.6

the long axis of the hind foot, yet still allows some limited inversion/eversion as the foot accommodates to uneven ground. Other than this adjustment to the substrate, the hind foot of wolf and temnocyonines is committed to fore-aft flexion/extension at the ankle joint (1° of rotational freedom at the tibio-astragalar articulation).

Metatarsals and Phalanges: A remarkable modification of the metatarsals of the hind foot can be documented for *Temnocyon* and *Delotrochanter* and is likely in *Mammacyon*. This involves the near loss of the first metatarsal and marked reduction of metatarsals 2 and 5, resulting in a strongly paraxonic hind foot in which metatarsals 3–4 bear the weight in the erect digitigrade stance (fig. 61A). In *Temnocyon ferox*, *Mammacyon obtusidens*, and *Delotrochanter oryktes*, the metatarsals are proximally appressed as is evident in large living canines (fig. 63).

Representation of temnocyonine metatarsals is shown in table 8: In *Temnocyon altigenis* (UCMP 9999) only metatarsal 2 is complete, with proximal parts of metatarsals 3–4 and distal metatarsal 1; in *T. ferox* (YPM-PU 10787) metatarsals 1–5 survived; in *Mammacyon obtusidens* (ACM 34-41) metatarsals 3–5; and in *M. ferocior* (F:AM 27562) only a complete metatarsal 2, a proximal metatarsal 5, and metatarsal 3 lacking the proximal end were recovered. For *D. oryktes* (UNSM 47800, CM 1589b) there are metatarsals 2–5. Feet of the large species of *Temnocyon* are unknown but similar cursorial adaptations are likely, given the derived hind foot anatomy of *T. ferox*.

All of these temnocyonine metatarsals indicate a paraxonic hind foot with elongate metatarsals 3–4 and shorter, more slender metatarsals 2 and 5. The most complete hind foot (fig. 61), that of *T. ferox*, shows metatarsals 2 and 5 to be ~1 cm shorter than metatarsals 3–4, with metatarsal 5 even more reduced than metatarsal 2. Metatarsal 1 also shows marked reduction (length, 45 mm; midshaft width, 4.8 mm). *Delotrochanter oryktes* exhibits even greater reduction of metatarsals 2 and 5, more so than in the wolf (fig. 63). Although the first metatarsal was not recovered, the scar for it on metatarsal 2 shows it was quite reduced, nonfunctional, yet not as small as the minute bone known in the canid. Metatarsal 2 of *M. ferocior* lacks an obvious scar for metatarsal 1 and so reduction of the latter bone in that species likely exceeded the state in *D. oryktes* and possibly equalled that found in the wolf. Reduction of the metatarsals flanking the paraxonic metatarsals 3–4 in *D. oryktes* is the most pronounced in the subfamily; consequently this reduction also probably occurred in *D. major*.

The lengths of paraxonic metatarsals relative to metacarpals are similar to those proportions in the wolf. In *T. ferox* where this can be measured, metatarsals 3–4 are 16%–17% longer than metacarpals 3–4, and in *D. oryktes* (UNSM 47800) this is 9%–10%,

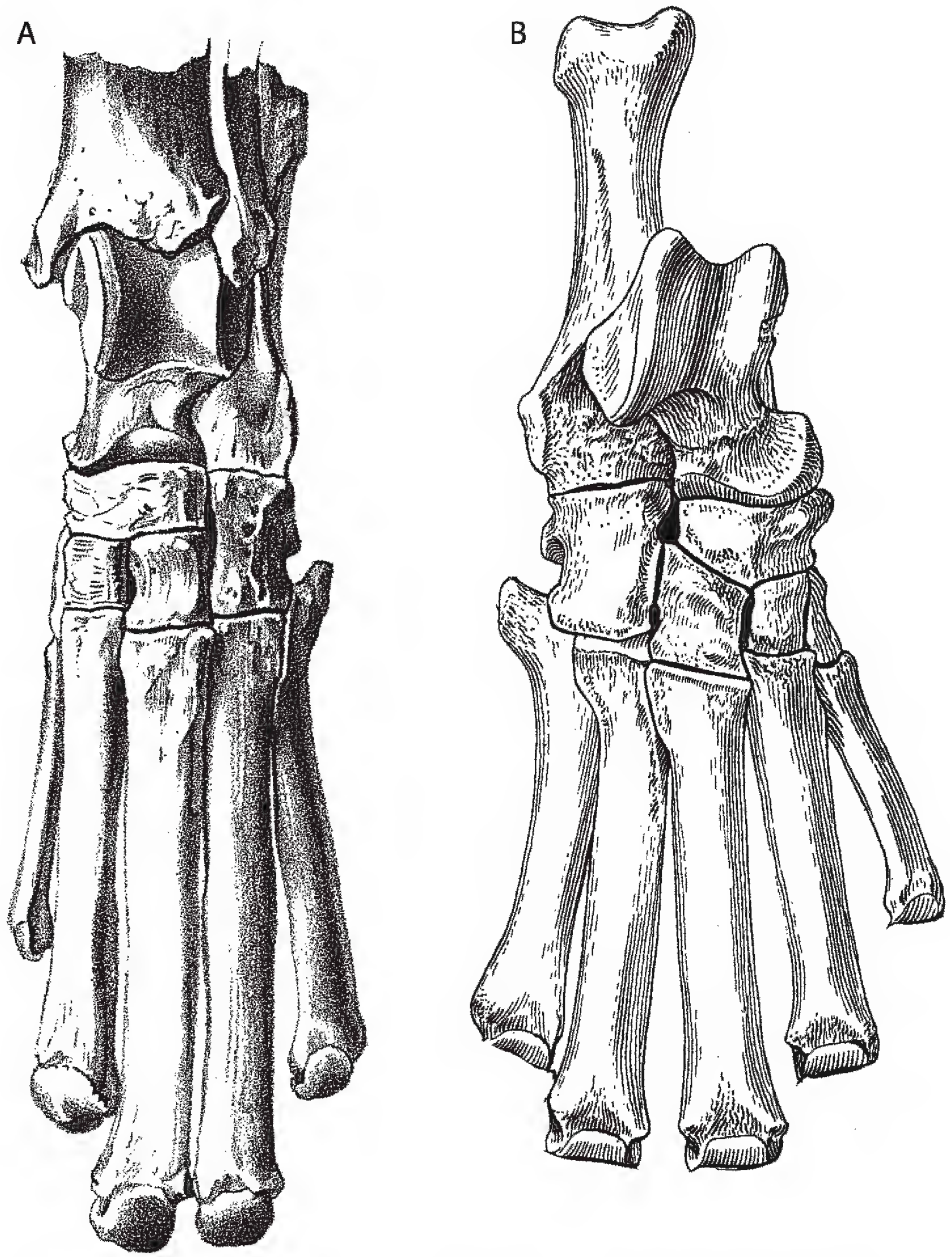


Fig. 61. Hind foot of (**A**) *Temnocyon ferox* (YPM-PU 10787) and (**B**) *Daphoenodon superbus* (CM 1589). The narrow columnar tarsus and appressed metatarsals in the cursorial temnocyonine differ from the more splayed and mobile foot of the daphoenine. *T. ferox* after Eyerman (1896); *D. superbus* after Peterson (1910).

whereas in the wolf the difference is 10%–13%, a clear indication of the elongation of the forefoot in *Delotrochanter*.

Metapodials of these temnocyonines have prominent, sharp distal keels that fit into a groove at the base of each proximal phalanx (fig. 56). A pair of sesamoid bones within the tendons of each interosseous muscle would have bordered each keel in the articulated hind foot of *Temnocyon ferox* and together

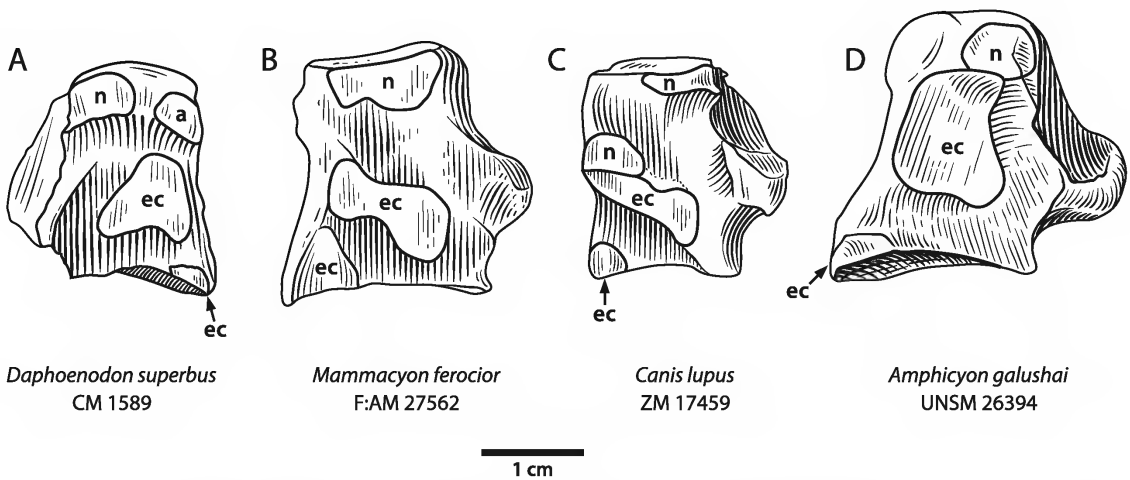


Fig. 62. Comparison of the cuboids of (**A**) *Daphoenodon superbus*, (**B**) *Mammacyon ferocior*, (**C**) *Canis lupus*, and (**D**) *Amphicyon galushai*. In temnocyonines and daphoenines, the proximal (upper) ectocuneiform facet (**ec**) is well separated from the navicular facet (**n**) but in *Amphicyon* they are confluent. The wolf cuboid has two navicular facets, one in direct contact with the ectocuneiform facet. In *D. superbus* the cuboid also contacts the astragalus (**a**), likely the plesiomorphic state in both daphoenines and temnocyonines. A, left cuboid; B, C, D, right.

with the grooved phalanx would help to align and stabilize the digits. The position of the keel permits extension but little flexion at the metapodial-phalangeal joint. The metapodial-phalangeal joint is prevented from hyperextension in the erect digitigrade stance by contraction of the interosseous and digital flexor muscles.

Reduction of the side-toes in these temnocyonines (*Temnocyon ferox*, *Delotrochanter oryktes*, and less complete remains of *Mammacyon*) parallels reduction in the wolf and other large cursorial canines and is the first example of this type of paraxonic hind foot to evolve in the Carnivora.

No phalanges certainly attributable to the hind foot of temnocyonines were recovered with the exception of much reduced, intermediate (length, 15 mm) and ungual (length, ~13 mm) phalanges of digit 5 in *T. ferox*. This suggests, however, that the intermediate phalanges in the hind foot were quite short, as in the forefoot. Eleven proximal and six intermediate phalanges and one ungual were recovered with the skeleton of *D. oryktes* (ACM 4804), but attribution to fore- or hind feet was not recorded (Schlain, 1980). These proximal phalanges are shorter, not as slender, and more robust than those of the wolf. Intermediate phalanges are uniformly short and somewhat asymmetrical; the distal trochlea extends proximad on the dorsal surface, indicating a moderate ungual retractility similar to that of the wolf.

The claws of *T. ferox* do not appear to have been very long. In the wolf, the keratin sheath covering the ungual phalanx adds ~50% to its length so that in *T. ferox*, if similar, the functional claw on digit 5 of the hindfoot would measure ~21 mm in length. This does not give us the length of the claw on a paraxonic digit of the hind foot; however, digit 4 of the forefoot also retains an ungual of similar size, suggesting that the claw length might have been about the same on the paraxonic digits of both fore- and hind feet. This situation is in conformity with the wolf where claws on fore- and hind feet are of similar lengths.

BASICRANIAL ANATOMY

Basicrania of temnocyonines are rarely preserved. Those that are known demonstrate that a plesiomorphic amphicyonid auditory region survived in those species (table 17). However, basicranial detail is often lacking and in most temnocyonines the auditory bulla has been lost prior to burial because it was not ankylosed to the

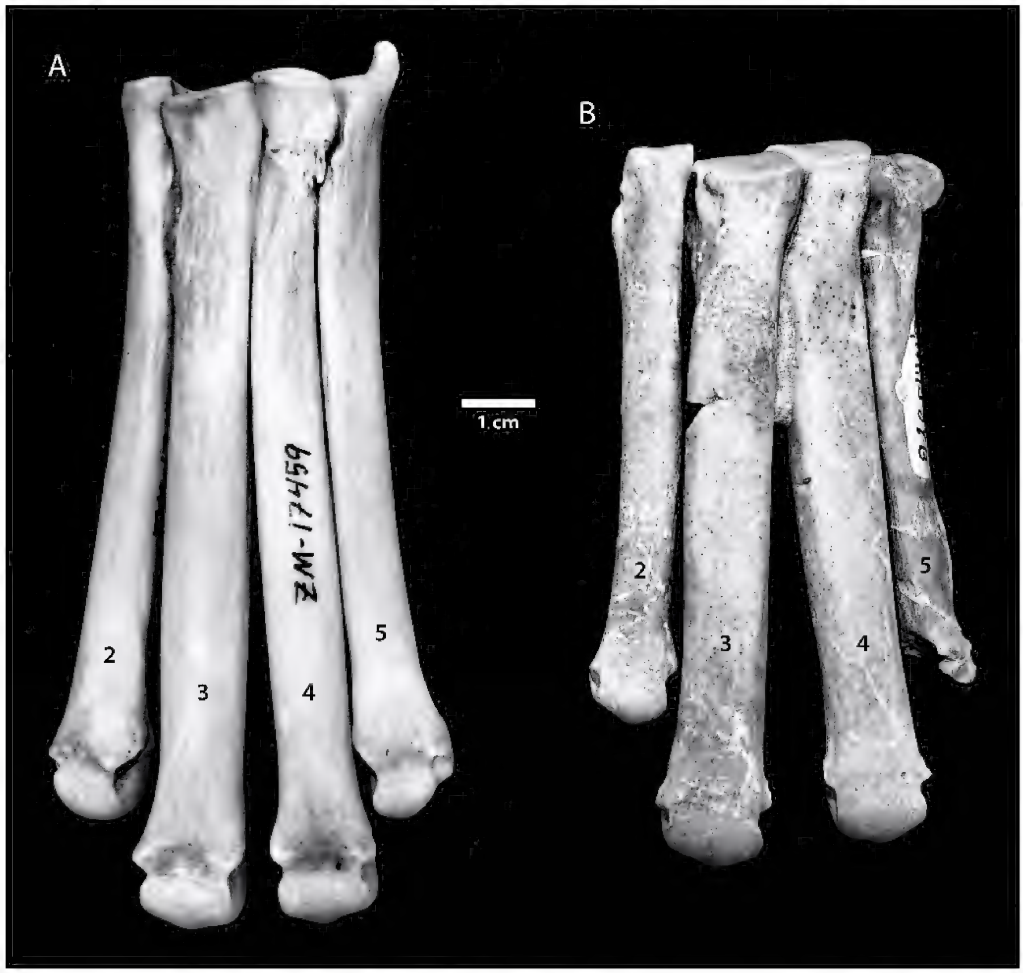


Fig. 63. Metatarsals 2–5 of *Canis lupus* (**A**) and *Delotrochanter oryktes* (**B**). Paraxonic metatarsals 3–4 are flanked by markedly reduced metatarsals 2 and 5 in *D. oryktes* (UNSM 47800), indicating a narrow hind foot.

skull. In a few individuals the fragile bulla remained attached to the skull: its form and composition in *Temnocyon subferox* and *Mammacyon obtusidens* are comparable to the rudimentary plesiomorphic bullae of the stem amphicyonids, *Daphoenus* and *Cynodictis* (fig. 64).

Intact temnocyonine basicrania show the embayed basioccipital typical of amphicyonid carnivores. Medial to the petrosal, the margin

TABLE 17
Temnocyonine Species with Preservation of Basicranial Morphology

Taxon	Mus. No.	Basioccipital embayment	Auditory bulla	Petrosal
Temnocyon altigenis	UCMP 9999	Yes	No	Yes
Temnocyon subferox	YPM 10065	Yes	Yes	Yes
Temnocyon fingeruti	NM 280/61	Yes	Yes	Yes
Mammacyon obtusidens	ACM 34-41	Yes	Yes	Yes
Mammacyon ferocior	F:AM 54134	Yes	No	No
Delotrochanter oryktes	ACM 4084	Yes	No	Yes

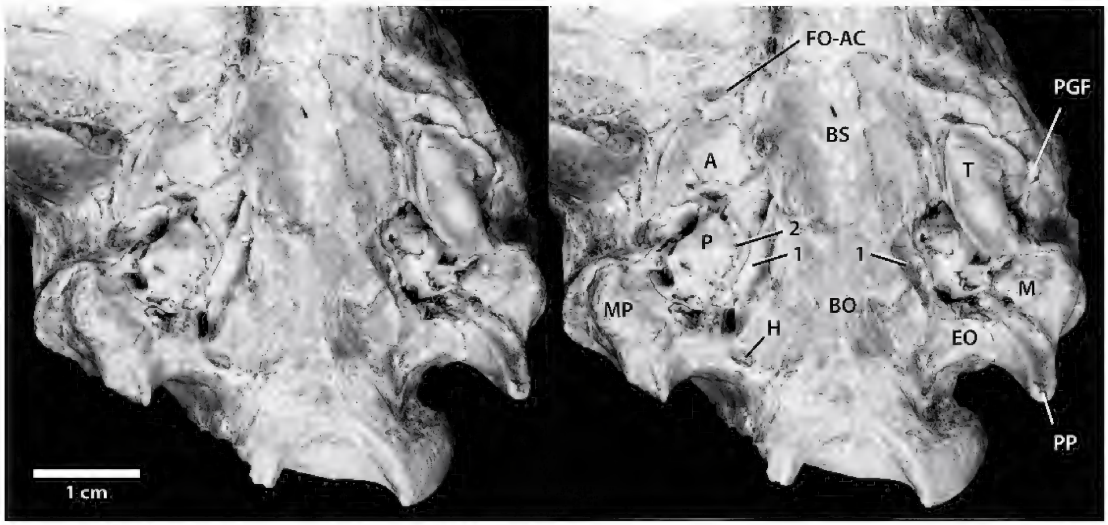


Fig. 64. Basicranium of the holotype of *Daphoenus vetus* Leidy (USNM 658, stereopair), White River Group, South Dakota, with auditory bulla formed by ectotympanic crescent (T). The margins of the basioccipital bone reveal the embayment for the inferior petrosal venous sinus (**1**). A cancellous medial wall of the promontorium (**2**) is broken open forming a ledge contacting the basioccipital. For abbreviations, see page 5.

of the amphicyonid basioccipital bone is pocketed by a deep recess (fig. 64, #1), presumably for the inferior petrosal venous sinus containing a loop of the internal carotid artery, functioning as a counter-current heat exchange mechanism (Hunt, 1977; Hunt and Barnes, 1994). In temnocyonines this embayment for the sinus presents as a deep semicircular pocket penetrating far into the basioccipital. The embayment is found in the most plesiomorphic temnocyonine, *Temnocyon altigenis* (UCMP 9999), in which the floor of the sinus is open to view, revealing its shape and dimensions (fig. 65, C/IPS). It is also developed in *T. subferox* and *T. fingeruti* and occurs in the holotype of *Mammacyon obtusidens* (ACM 34-41); in the skull of the large *Mammacyon ferocior* (F:AM 54134); and in *Delotrochanter oryktes* (ACM 4804). Thus, a deeply embayed basioccipital is characteristic of the subfamily and was present in the earliest temnocyonines.

The petrosals of temnocyonines and *Daphoenus* are defined by a low, rounded, pear-shaped promontorium (fig. 65, UCMP 9999), and are similar in form in the five temnocyonine species where they are preserved (table 17). As in *Daphoenus*, the temnocyonine petrosal in mature adults can appear slightly rugose where the bulla contacts the promontorium along its medial margin, but it lacks the prominent ventral process found in aeluroid carnivorans (Hunt, 1989). Previously described North American amphicyonids belonging to daphoenine and amphicyonine subfamilies have petrosals with promontoria of this type. The promontorium in ventral view is posteriorly broad, tapering as it slopes anteriorly to a blunt terminus in the anteromedial corner of the auditory region. Dimensions of the promontoria (length, width) reflect the increase in size of these species: (*T. altigenis*, 10.6, 7.8 mm; *T. subferox*, ~12, 9.5 mm; *M. obtusidens*, 12.3, 9.9 mm; *D. oryktes*, 12.4, 11.4 mm). The tegmen tympani, although damaged to some degree in all these skulls, is anatomically similar to the tegmen of *Daphoenus* in that the the fossa muscularis major, epitympanic recess, path for the facial nerve, and stapedius fossa are of the same plesiomorphic configuration and proportions, and the middle ear space does not invade surrounding basicranial bones.

The most remarkable anatomical trait of the temnocyonine basicranium is the rudimentary condition of the auditory bulla in these carnivores. The temnocyonine bulla

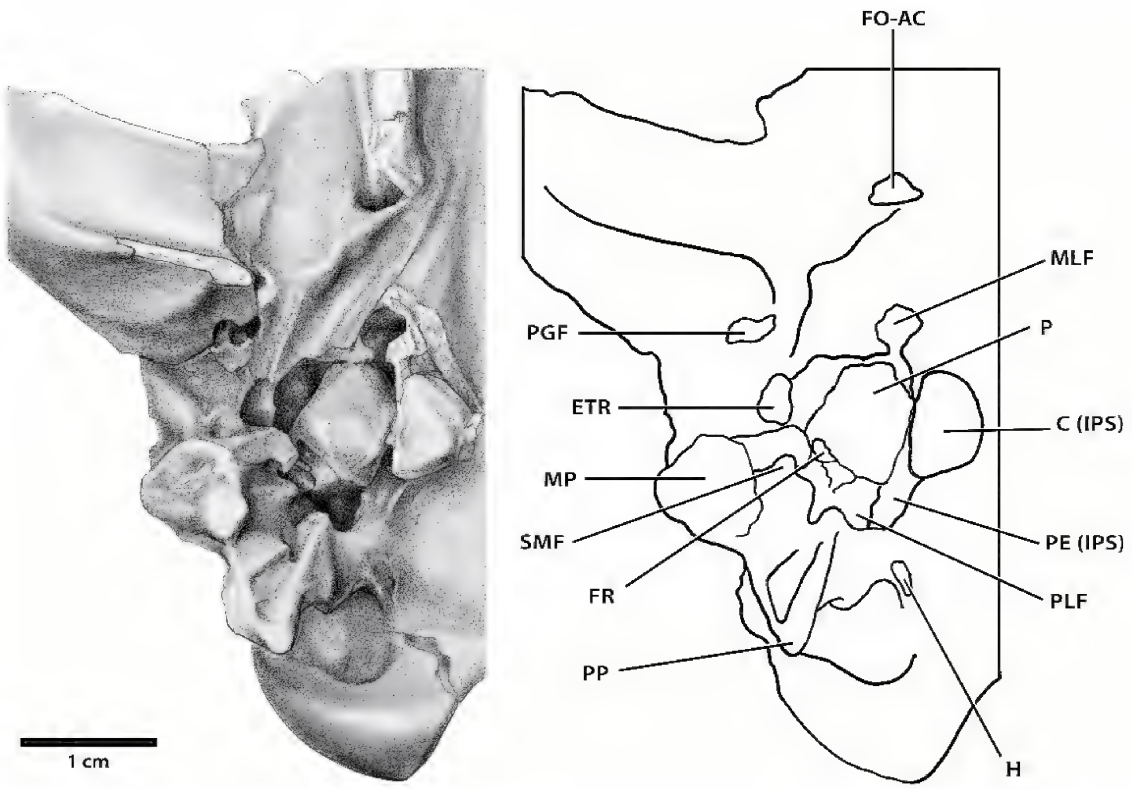


Fig. 65. Basicranium of the Logan Butte *Temnocyon altigenis* (UCMP 9999): the basioccipital has been opened to show sediment [C(IPS)] filling the deep embayment in the bone for the inferior petrosal venous sinus characteristic of temnocyonines. For abbreviations, see page 5.

was previously unknown and survives in only three species: *Temnocyon subferox* (YPM 10065); *Mammacyon obtusidens* (ACM 34-41); and *T. fingeruti* (NM 280/61). These bullae are little derived beyond the plesiomorphic state seen in the earliest daphoenines and are among the most plesiomorphic auditory bullae of North American amphicyonids, their small size and lack of development atypical for such large carnivorans.

Species of *Daphoenus* and *Cynodictis* demonstrate the most primitive state of the amphicyonid auditory bulla, a simple osseous ectotympanic crescent loosely attached to the skull (fig. 64, T). If rostral or caudal entotympanics were present, they were hyaline or fibrocartilaginous elements that formed a medial wall of the bulla. A cartilaginous caudal entotympanic would have been restricted to a narrow space between the inner edge of the ectotympanic and the petrosal, a space defined in life by the orientation of the bony ectotympanic crescent. In *Daphoenus vetus* a cartilaginous caudal entotympanic was almost certainly joined to the medial border of the osseous ectotympanic. It attached to a thin rim along the inner inflected edge of the ectotympanic and also to the surface of the petrosal promontorium and did not ossify during the life of the carnivore (fig. 64). These primitive amphicyonid bullae show no expansion of the ectotympanic in order to more completely enclose the middle ear space. They must have functioned much like the similarly constructed bullae of the living African palm civet (*Nandinia binotata*) in which a bony ectotympanic crescent, joined to a hyaline cartilage caudal entotympanic, together enclose a middle ear of small volume.

Figures 66 and 67 illustrate the auditory bullae of *Temnocyon subferox* and *Mammacyon obtusidens*. In both, the bulla is attached to the skull in the same manner as in

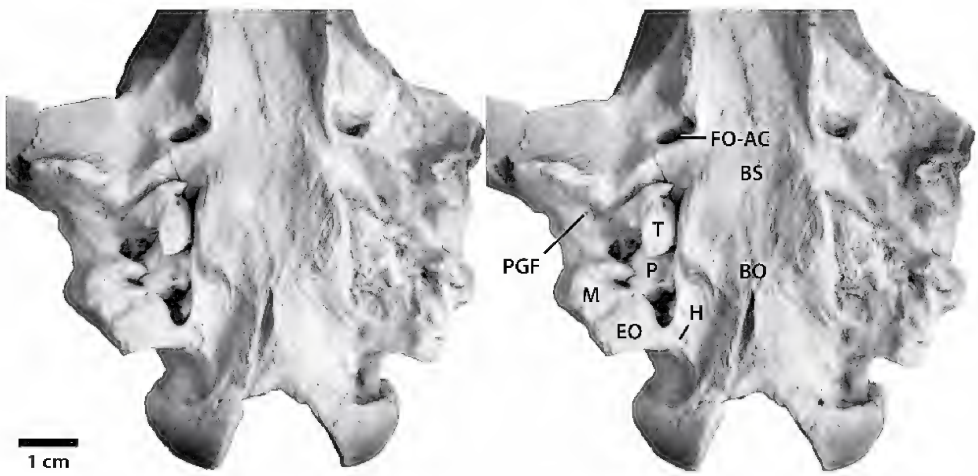


Fig. 66. Holotype basicranium of *Temnocyon subferox* (YPM 10065), John Day Formation, Oregon (stereopair). The bulla fragment in the auditory region is a remnant of an ectotympanic crescent (T) similar to that seen in *Daphoenus*. YPM 10065 represents the plesiomorphic state of the temnocyonine auditory bulla. For abbreviations, see page 5.

Daphoenus and *Cynodictis*. In *Daphoenus vetus* (fig. 64) the anterior crus of the ectotympanic fits in a small circular depression medial to the postglenoid foramen of the squamosal. The posterior crus attaches to the posttympanic process of the squamosal that forms the anterior margin of the mastoid process. These squamosal attachments for the anterior and posterior crura are the plesiomorphic contacts of the ectotympanic with the skull for species of the Order Carnivora.

In more evolved daphoenines and amphicyonines, the ectotympanic crescent eventually expands to a more capsular bulla form. Whether the capsule incorporates entotympanic elements or is formed entirely by the expanded ectotympanic is uncertain in many adult amphicyonids since the bulla does not show convincing evidence of discrete entotympanics that form the medial and posterior walls of the capsule. Amphicyonid bullae commonly lack significant medial and/or posterior bulla inflation that might suggest the presence of an expanding entotympanic.

In *Temnocyon subferox* (YPM 10065) the ectotympanic represents the most plesiomorphic state recognized in the subfamily (fig. 66). Here a small ectotympanic fragment, nearly situated as in life, with a width of only a few mm (14 mm from tip of anterior crus to inner margin of the crescent; 6 mm width at center of crescent), shows that the crescent and attached tympanic membrane would have been positioned directly below (ventral to) the petrosal delimiting a relatively small middle ear space. Although the posterior half of the crescent is missing, the remaining anterior half shows that there could have been no expansion of the middle ear posterior to the petrosal. There is also no extension of the ectotympanic to form an osseous external auditory meatus. This is essentially the same ectotympanic configuration as in *Daphoenus* and *Cynodictis*. In YPM 10065 the crescent has been slightly displaced postmortem so that its medial margin approaches the promontorium. If restored to its correct placement, a small space for an elliptical caudal entotympanic element configured as in *Daphoenus* is available; this entotympanic would contact a low, narrow ridge on the medial border of the promontorium.

In *Mammacyon obtusidens* (ACM 34-41), as in *T. subferox*, only the anterior half of the ectotympanic has survived, yet in ACM 34-41 this remnant is in its life position (fig. 67). In both species the alignment of the tympanic membrane was similar, oriented at ~45° from the horizontal. The width of the bulla of *M. obtusidens* measured from the external meatal aperture to the bulla's medial wall is only 5 mm; the tympanic crista occupies 2.2 mm of this distance, its thin margin positioned only 2.8 mm from the medial wall,

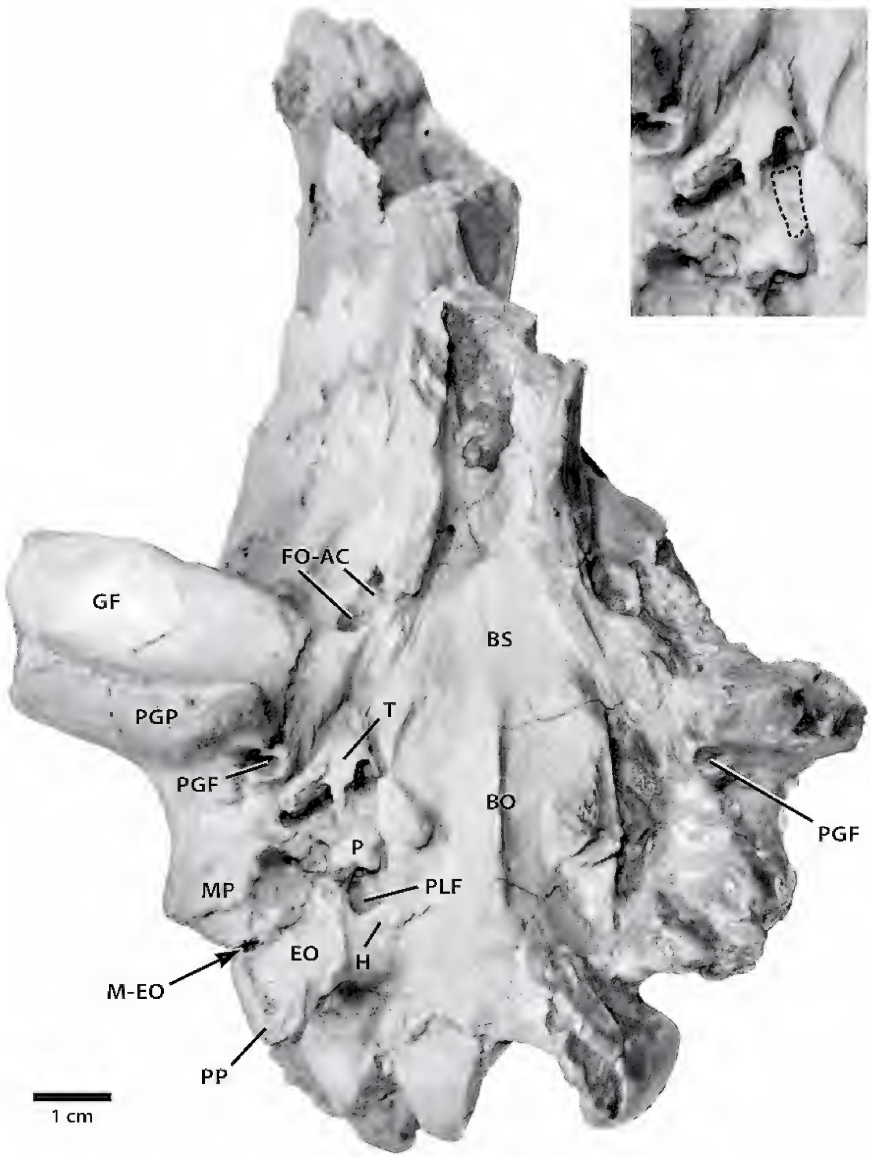


Fig. 67. Holotype basicranium of *Mammacyon obtusidens* (ACM 34-41) with the remnant of the ectotympanic auditory bulla (T) in life position. The posterior portion of the bulla was lost but contacted the medial margin of the promontorium (P), evidenced at that location by a shallow depression (indicated by dashed line on inset). For abbreviations, see page 5.

indicating the extremely small volume of the auditory bulla and middle ear. There was no bony external auditory meatus; here, as in *T. subferox* and *Daphoenus*, the meatal tube must have been cartilaginous. Remarkably, ACM 34-41 preserves a vestige of the inner (medial) wall of the bulla: an extremely thin osseous lamina resting on the medial edge of the petrosal promontorium. The surface of the promontorium displays a shallow linear depression that receives this bony lamina, once part of a continuous partition forming the medial wall. The identity of the ontogenetic element (ecto- or entotympanic) making up the medial bulla wall is uncertain.

The basicranium of *Temnocyon fingeruti* (NM 280/61) includes both auditory bullae (fig. 68), the left one intact, the best preserved

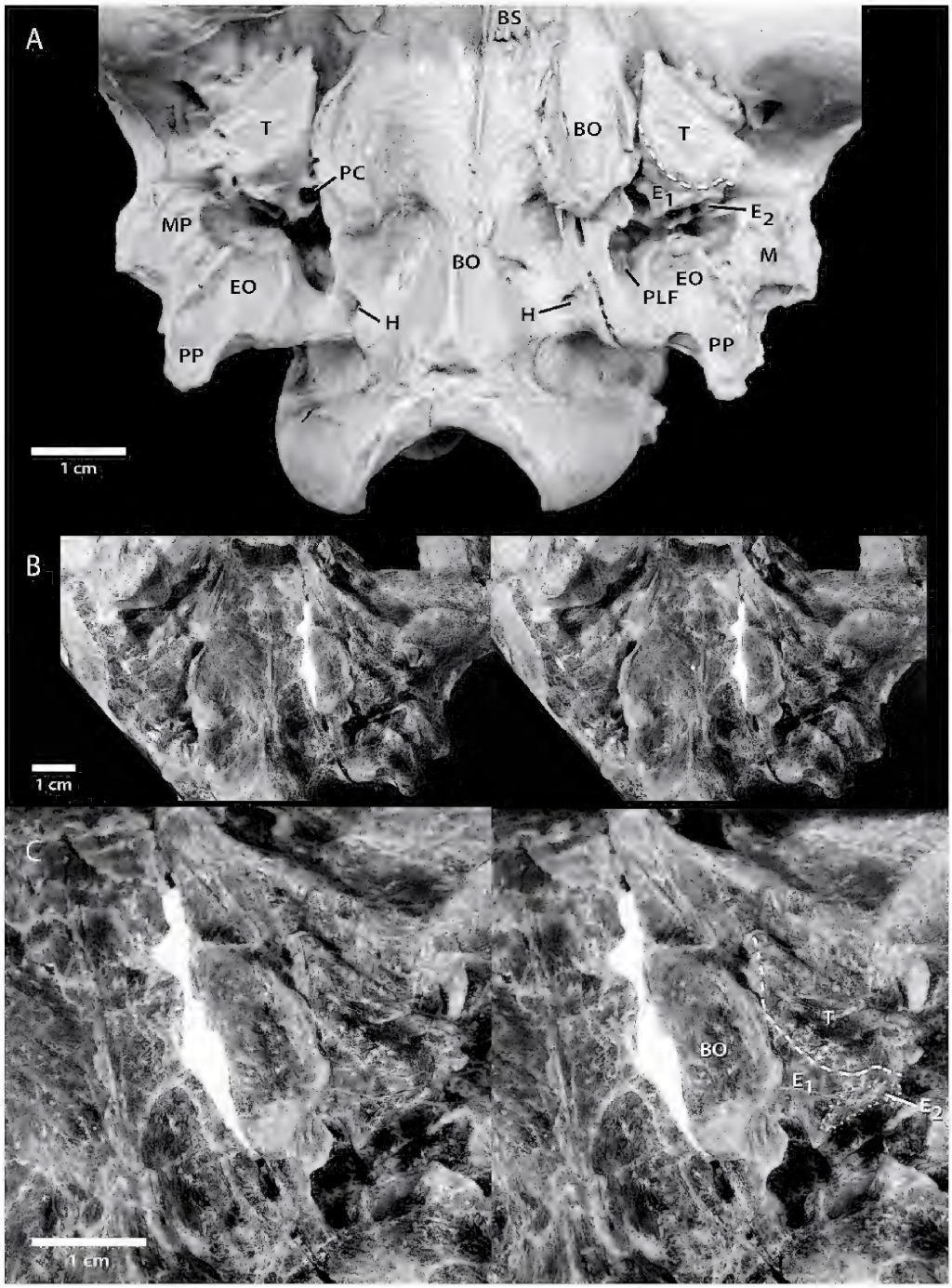


Fig. 68. Holotype basicranium of *Temnocyon fingeruti* (NM 280/61), Balm Creek, Haystack Valley Member (revised), John Day Formation, Wheeler Co., Oregon. **A,** epoxy cast of basicranium showing left and right auditory bullae each composed of an ectotympanic, an E_1 caudal entotympanic forming the medial wall, and an E_2 caudal entotympanic completing the posterior wall of the bulla. **B,** basicranium of NM 280/61 in ventral view (stereopair). **C,** detail of the auditory region and the principal bulla elements (stereopair). For abbreviations, see page 5.

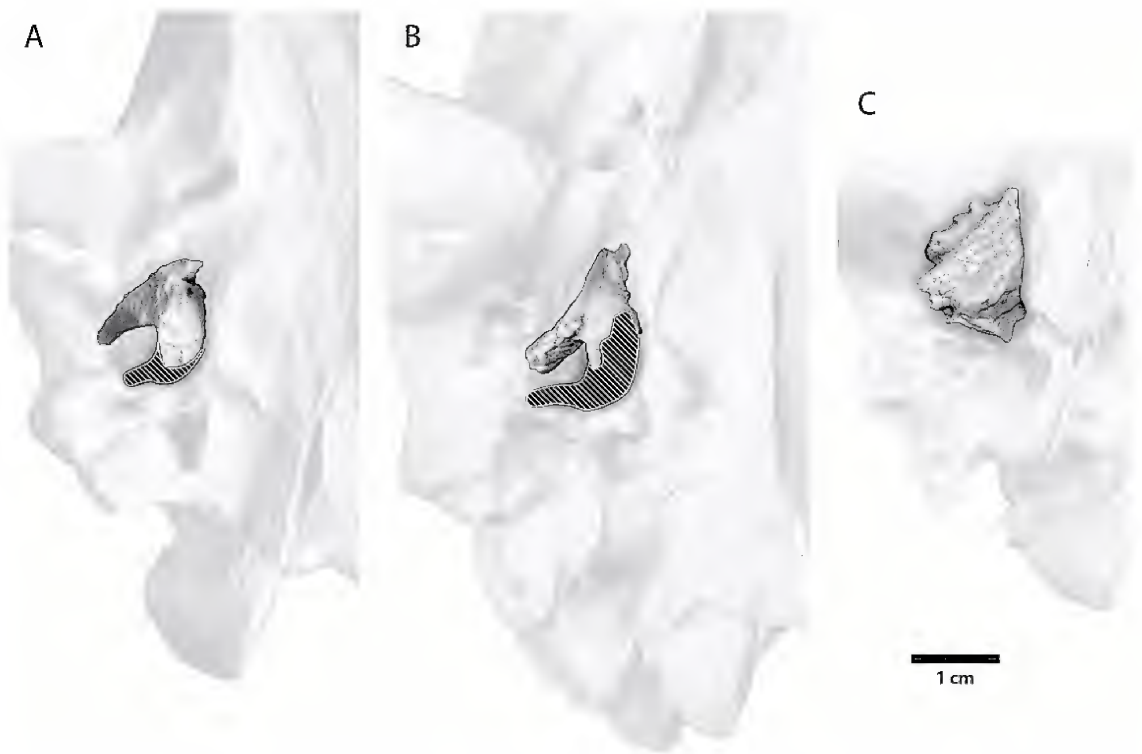


Fig. 69. Evolution of the auditory bulla in temnocyonines: **A,** plesiomorphic ectotympanic crescent in *Temnocyon subferox*; **B,** a larger ectotympanic with styloid process in *Mammacyon obtusidens*; **C,** a small capsular rudimentary bulla in *Temnocyon fingeruti* enclosing the middle ear and formed by an ectotympanic (T) and two caudal entotympanic (E_1, E_2) elements. These bullae are only loosely attached to the skull. Posterior part of **A** and **B** restored as in life (cross-hatched).

of any temnocyonine, and more derived than the bullae of *T. ferox* and *M. obtusidens*. The bullae of YPM 10065, ACM 34-41, and NM 280/61 comprise an anatomical progression demonstrating the progressive enclosure of the temnocyonine middle ear (fig. 69). Although achieving complete enclosure in *T. fingeruti*, the middle ear volume is quite small, and the species fails to evolve the large, inflated, well-ossified and often firmly ankylosed bullae of many living carnivorans that enclose a much larger middle ear space.

The auditory bulla of *Temnocyon fingeruti* is critical to interpretation of the temnocyonine middle ear. In NM 280/61 the bullae are situated as in life. Their relationship to the remainder of the basicranium shows that they are unusually small relative to the size of the skull. Although the middle ear is fully enclosed by the bulla, the bony capsule is rudimentary, only slightly evolved beyond that inferred for *M. obtusidens*. Bulla inflation or other enlargement of the capsule to enclose an expanded middle ear cavity does not occur, middle ear volume is minimal, and the bony bulla does not extend behind (posterior to) the mastoid process. Here the contribution to the osseous bulla by the ectotympanic and two caudal entotympanics is evident from the surface configuration of the bulla. The anterior part of the bulla is formed entirely by the ectotympanic (fig. 68, T), including a short osseous external auditory meatus. Fused to the medial edge of the ectotympanic is an ossified caudal entotympanic, forming the medial wall of the bulla (fig. 68, E_1), which in its anterior part is nearly vertical but posteriorly becomes broader and outwardly convex at the posteromedial corner of the bulla, partly enclosing the posterior carotid foramen for the internal carotid artery.

The suture between ecto- and caudal entotympanic (E_1) traverses the bulla surface from its anteromedial to posterolateral corner, marking the line of fusion between the two elements (fig. 68A, 68C, dashed line). As in several living arctoid carnivorans (Hunt, 1974), a small elliptical ossification is applied to the posterior margin of the E_1 caudal entotympanic to complete the bulla's posterior wall. This small element, evident in both bullae, appears to be a posterior caudal entotympanic or E_2 element (fig. 68) like that known in *Ursus americanus* (Hunt, 1974: pl. 4). It fuses to the E_1 caudal entotympanic that forms the medial wall. As such, the *T. fingeruti* bulla shows a similar disposition of ontogenetic elements as in living ursids. This pattern is also seen in some pinnipeds, procyonids, and mustelids and in the ailurid lesser panda *Ailurus fulgens* (Hunt, 1974: pls. 6, 8, 9; Hunt and Barnes, 1994). Rather than evidence of close relationship with ursids, these auditory bullae reflect retention of an early plesiomorphic stage in the development of the arctoid bulla.

The relevant anatomical characteristics of the temnocyonine auditory region are: (a) an extremely rudimentary bulla capsule, at first (*Temnocyon subferox*) formed by an ectotympanic crescent, probably with an initial cartilaginous entotympanic contribution; then (*M. obtusidens*) incorporating weak ossification of the medial bulla wall; and later (*T. fingeruti*) by ossification of caudal entotympanic (E_1 and E_2) elements fusing with the ectotympanic to form a fully ossified auditory bulla; (b) absence of inflation of the bulla capsule despite increasing body size, resulting in a middle ear space of very small volume; (c) absence of a prominent bony external auditory meatus in *T. ferox* and *M. obtusidens*, incipient in *T. fingeruti*; (d) failure of the bulla to extend backward in the auditory region behind the mastoid process (the posterior carotid foramen marks the posterior extent of the bulla in *T. fingeruti*, as in many living ursids); (e) no bulla contact with the exoccipital bone and its paroccipital process; (f) presence of the deep embayment in the margin of the basioccipital bone for the inferior petrosal venous sinus.

These temnocyonine bullae can be distinguished from the auditory bullae of large daphoenine and amphicyonine beardogs, yet these amphicyonid subfamilies apparently all evolved from stem arctoid carnivores with a plesiomorphic auditory region, perhaps much like those of *Daphoenus* and *Cynodictis*. The rudimentary auditory bullae of YPM 10065, ACM 34-41, and NM 280/61 (fig. 69) suggest that development of a well-ossified capsular enclosure for the middle ear was retarded in the phylogeny of the Temnocyoninae relative to many small contemporary arctoid and cynoid carnivorans. Many canids by the late Oligocene had fully enclosed their auditory regions in an osseous bulla capsule firmly attached (even ankylosed) to the basicranium and made up of moderately to well-inflated ecto- and entotympanic elements. These temnocyonine skulls show that even by ~23.8 Ma in the latest Oligocene, the *Temnocyon* lineage had not yet evolved a middle ear volume even approaching the greater volumes found in large living carnivores of similar body mass; such expanded bullae presumably enclose a middle ear capable of more sensitive frequency-enhanced audition (Hunt and Korth, 1980; Stebbins, 1983; Rosowski, 1994). It is possible that temnocyonines may not have acquired a capability for perception of low-frequency sound, if a small middle ear volume damped mobility of the auditory ossicles. We do not know if the plesiomorphic bullae of the Oligocene temnocyonines were retained or possibly "improved" in the early Miocene species: auditory bullae and intact basicrania have not been found for *Temnocyon macrogenys* and *T. percussor*, or for *Delotrochanter major* and *D. oryktes*, or even for the latest Oligocene *Mammacyon ferocior*.

AGE AND CORRELATION

Radioisotopic and Biochronologic Calibration of Temnocyonine Sites

Although the provenance of some temnocyonines was never recorded or has been lost, a significant number were found in proximity to volcanic tuffs or ignimbrites that have been radioisotopically dated by the $^{40}Ar/^{39}Ar$ or K/Ar methods. These occurrences, in company with faunal associations and known stratigraphic placements, are the basis

for the temporal range diagram presented here (fig. 70). In the John Day region *Temnocyon altigenis* (UCMP 1549, 9999), *T. fingeruti* (NM 280/61), *Mammacyon obtusidens* (LACM 5386), and *Rudiocyon amplidens* (LACM 480) were found in proximity to dated stratigraphic horizons. Similarly, in the Great Plains, the temnocyonines from sites along the Niobrara River in the vicinity of Agate Fossil Beds National Monument occur in an established stratigraphic relationship to the Agate Ash, a consolidated tuff dated repeatedly since 1964. References for dated tuffs and ignimbrites are listed in Tedford et al. (2004: 219–221) or are mentioned here.

John Day Basin

The geologically oldest records of John Day temnocyonines are the reports of *Temnocyon altigenis* (Merriam, 1906) at Logan Butte (UCMP 9999, locality 898), and near the village of Monument (UCMP 1549, locality 874) along the north fork of the John Day River (see Fisher and Wilcox, 1960; Wilcox and Fisher, 1966). Locality 874 is a low bluff where gray to olive-buff volcaniclastic sediments are exposed below the capping Picture Gorge ignimbrite (28.7 Ma); the gray fine-grained tuffaceous sandstone adhering to the skull suggests that UCMP 1549 was collected from gray beds directly below the ignimbrite. At Logan Butte, 75 mi southwest of Monument, a number of superposed, dated tuffs are interbedded with John Day rocks that form the butte and adjacent badlands (T. Fremd, personal commun., 1994); here the youngest tuff, near the top of the stratigraphic section at the butte, dates at 28.87 Ma. *Temnocyon altigenis* (UCMP 9999) comes from badlands below this stratigraphic level that include tuffs dated at 29.11 and 29.25 Ma. These two *T. altigenis* skulls, both from the lower John Day Formation, are the only individuals of this species found in proximity to radioisotopically dated beds. The Logan Butte occurrence (UCMP 9999) establishes the approximate time of origin of the subfamily. The holotype of *T. altigenis* (AMNH 6855) and other mandibles of the species found in the 19th century cannot be placed in a stratigraphic context except to state that the patina and mineralization of these jaws suggests they also came from lower John Day sediments.

The skull of *Temnocyon subferox* (YPM 10065) was collected from the "Middle John Day" Formation, possibly late in the 19th century by a collector in the employ of O.C. Marsh, and is without precise stratigraphic or geographic information. A pale gray, very fine tuffaceous sandstone is present within the braincase. Although its age is uncertain, it was probably collected from John Day rocks above the Picture Gorge ignimbrite (28.7 Ma). The larger size of the skull and more derived dentition support an age somewhat younger than the *T. altigenis* hypodigm.

An exact stratigraphic level is known for the skull of *Temnocyon fingeruti* (NM 280/61) collected in the Haystack Valley Member (as revised, Hunt and Stepleton, 2004) of the John Day Formation along Balm Creek. An $^{40}Ar/^{39}Ar$ date of ~23.8 Ma was obtained on sanidine from a tuffaceous siltstone 62 ft (19 m) beneath the beardog site (Hunt and Stepleton, 2004: 81). Sediments between the dated level and the beardog include fluvial channel conglomerate fining upward to tuffaceous sandstones and siltstones with immature paleosols that together represent a single, possibly brief depositional interval; thus the skull may be not much younger than the ~23.8 date. It is of latest Oligocene age.

Locality records at Princeton University state that the holotype skull and skeleton of *Temnocyon ferox* (YPM-PU 10787) was found "near Maginnis' ranch, Turtle Cove, John Day river, Oregon," collected in the "Upper John Day" by L.S. Davis in 1889. The skeleton is embedded in a gray fine tuffaceous sandstone, the bone a pale tan to light brown color. The skull's large size and derived dentition indicate a stratigraphic level above the Picture Gorge ignimbrite, most likely from gray sandstones of the Kimberly Member. However, our examination of Kimberly Member outcrops along Maginnis Creek, west of the John Day River (secs. 25, 26, 35, 36, T10S, R25E, Mt. Misery 7.5-minute quadrangle), led us to doubt that this area was the source of the holotype, as its rocks were unfossiliferous and somewhat inaccessible. Further research brought us to the Son Hill ranch, 2 mi northwest of

Kimberly on Oregon Highway 19. Here, Son Hill, related to the Hamilton Maginnis family by marriage, informed us that his ranch was the actual location of the 19th century Maginnis homestead. Fossiliferous gray tuffaceous sandstones assigned to the Kimberly Member occur in the vicinity of the Maginnis ranch and trend northwest from Kimberly for 3.6 mi (5.8 km) along Oregon Highway 19; this is a more probable, general locale for YPM-PU 10787. Gray tuffaceous sandstones attributed to the Kimberly Member range widely in age, from slightly younger than 25.9 Ma (Tin Roof tuff) to possibly as young as ~23 Ma along the John Day river south of Kimberly, and to 27.9 Ma (Deep Creek tuff) at Rudio Creek. *Temnocyon ferox* is clearly a more advanced species in skeletal and dental anatomy than *T. altigenis* and *T. subferox*. Because *T. ferox* is dentally similar yet less evolved than *T. percussor*, a species dated by the Agate Ash (22.9 Ma), an age older than ~23 Ma is likely for the Maginnis ranch beardog. Here the age of *T. ferox* is thought to fall somewhere between the Tin Roof tuff (25.9 Ma) and the occurrence at ~23.8 Ma of the more dentally advanced *T. fingeruti* at Balm Creek.

The mandible of *Rudiocyon amplidens* (LACM 480), the largest of the John Day temnocyonines, comes from California Institute of Technology (CIT) locality 31, "from gray beds east of the road, 1.5 to 2 miles south of the Johnson ranch at the mouth of Rudio Creek." Gray tuffaceous sandstones and siltstones of the Kimberly Member are the principal lithologies east of the road along the creek over this distance. The most probable source outcrop is a fluvial channel complex prominently exposed in a north-facing bluff situated 1.5 mi (2.4 km) south of the ranch in the NW4, NE4, NE4, sec. 27, T9S, R26E. Here an oreodont maxilla and other bone fragments having the same pale brown-buff color and mineralization as LACM 480 were found in these channel beds, which include fluvial conglomerate, friable gray tuffaceous sandstones and siltstones, clayey siltstone, clay lenses, and diatomite. At the base of the bluff only a few meters to the northeast is a consolidated ash thought to be equivalent to the Deep Creek tuff by R.V. Fisher during his mapping of the John Day Formation along Rudio Creek (Fisher and Rensberger, 1972: 14). The ash occurs 80–90 ft (~24–27 m) below the channel sediments that likely yielded LACM 480. If the ash is correctly attributed, the mandible and associated braincase of *Rudiocyon* are then younger than the Deep Creek tuff (~27.9 Ma) and occur at the approximate level of the stratigraphically higher Biotite tuff (27.18 Ma), which provides a plausible age estimate for *R. amplidens*.

Green tuffaceous sediment adhering to the maxilla of *Mammacyon obtusidens* (LACM 5386) from Haystack Valley indicates that it came from dark green claystones attributed to the Turtle Cove Member making up the floor of the valley (Hunt and Stepleton, 2004: 74, map E, *Tjt*). The maxilla was found at CIT locality 29, " a large exposure of green beds on the north side of Haystack Valley," which occurs in proximity to an outcrop of the Picture Gorge ignimbrite. Whether the maxilla came from above or below the ignimbrite is uncertain but the size and evolved state of the teeth support an age somewhat younger than 28.7 Ma, the age of the ash-flow.

Arikaree Group, Great Plains

The Great Plains temnocyonines are more difficult to place in a temporal context relative to most John Day species due to the scarcity of isotopically dated volcanic ash beds in the Arikaree rocks of northwest Nebraska and southeast Wyoming. Far removed from their source volcanoes, Arikaree tuffs are primarily vitric and extremely fine-grained, and often lack crystals amenable to radioisotopic analysis. The tuff known as the Agate Ash occurring within the Harrison Formation at Agate Fossil Beds National Monument in northwest Nebraska has been a frequently sampled principal calibration point (Evernden et al., 1964; Tedford et al., 1987: 198). Recently $^{40}Ar/^{39}Ar$ analysis on sanidine gave an age of 22.9 ± 0.08 Ma (Izett and Obradovich, 2001), placing the tuff immediately above the Oligocene-Miocene boundary (23.03 Ma, Lourens et al., 2004).

The Agate Ash establishes a reliable age estimate for the occurrence of *Temnocyon percussor* at nearby *Syndyoceras* Quarry, and

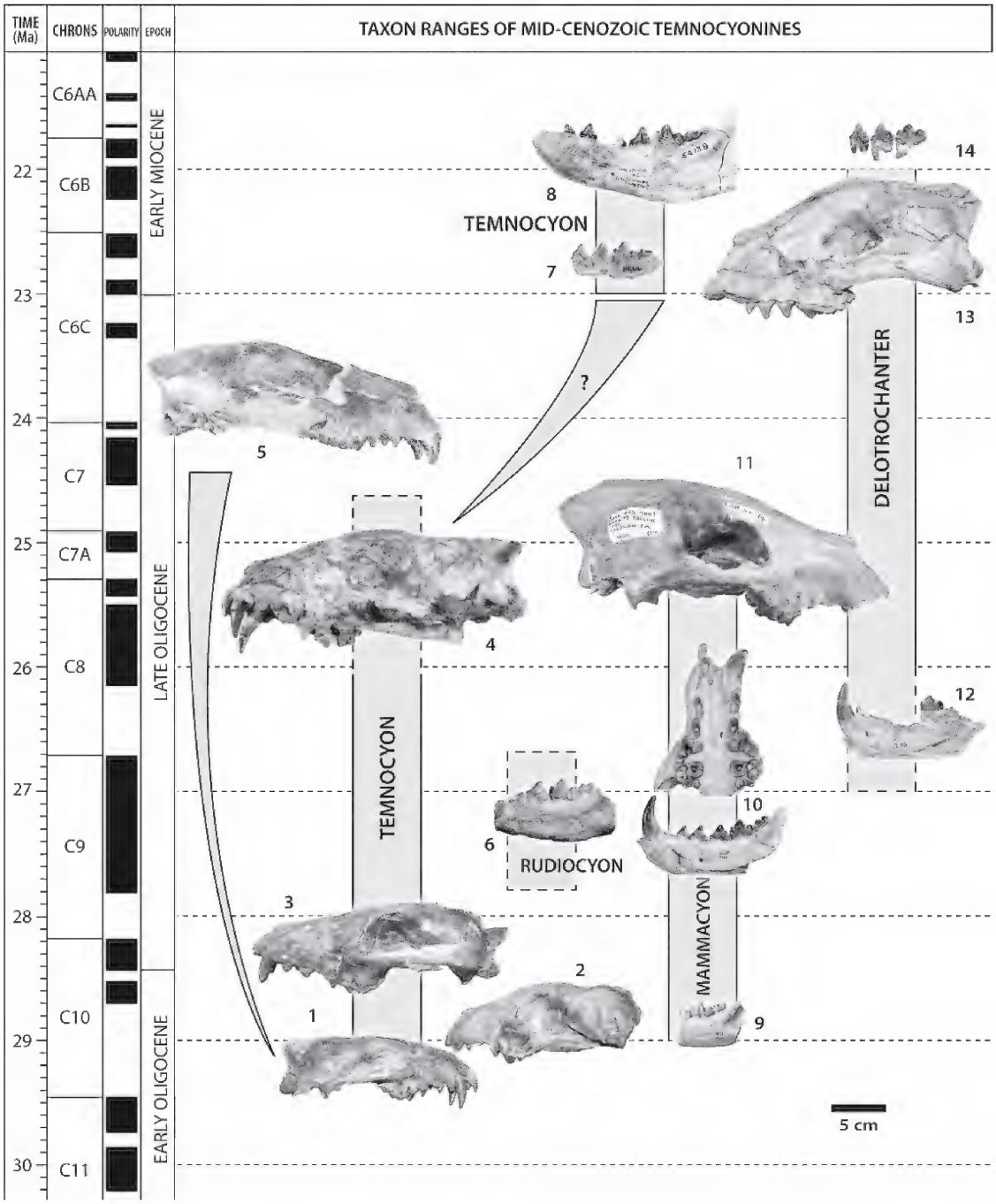


Fig. 70. Taxon ranges of North American temnocyonines in the Pacific Northwest and Great Plains. **1,** *Temnocyon altigenis* (Logan Butte); **2,** *T. altigenis*; **3,** *T. subferox*; **4,** *T. ferox*; **5,** *T. fingeruti*; **6,** *Rudiocyon amplidens*; **7,** *T. percussor*; **8,** *T. macrogenys*; **9,** cf. *Mammacyon* (Sharps Fm.); **10,** *M. obtusidens*; **11,** *M. ferocior*; **12,** *Delotrochanter petersoni*; **13,** *D. oryktes*; **14,** *D. major*. Placement for 3, 4, 6, and 12 are best estimates indicated by dashed lines. Numbers 1–6, John Day Formation; numbers 7–14, Great Plains. *Temnocyon* occurs chiefly in the John Day Formation of the Pacific Northwest; terminal species of the genus are from the Great Plains. *Mammacyon* and *Delotrochanter* are common in Arikaree Group

also for *Delotrochanter oryktes* at *Stenomylus* Quarry. Both quarries occur within the Harrison Formation in proximity to this tuff. The isolated teeth assigned to *T. percussor* from the AMNH-Cook Quarry, and the skull of *D. oryktes* from the carnivore den excavated into the Agate waterhole bonebed, come from the basal Anderson Ranch Formation, which is directly superposed on the Harrison Formation throughout the national monument. So these fossils are somewhat younger. The temporal separation appears to be geologically brief, given the similarity of the Harrison Formation fauna to the fauna from the waterhole bonebed on Carnegie and University Hills.

The geologically youngest species of *Temnocyon* and *Delotrochanter* (*T. macrogenys*, *D. major*) come from higher stratigraphic levels of the early Miocene Anderson Ranch Formation (Hunt, 1990, 2002b) in southeast Wyoming and northwest Nebraska. These are the last surviving temnocyonines in North America. There is little doubt that *T. macrogenys* and *D. major* are descended from the Harrison *T. percussor* and *D. oryktes*. Since they have evolved to a marked degree in size and dentition, it appears that substantial time has elapsed—previously a crystal-vitric tuff (Eagle Crag Ash, Hunt et al., 1983) has provided the only radiometric age (19.2 ± 0.5 Ma, fission track-zircon) for the Anderson Ranch Formation. Attempts to obtain an $^{40}Ar/^{39}Ar$ analysis on sanidine from this tuff have not been successful. However, zircons extracted from the tuff have undergone SHRIMP U-Pb analysis yielding a preliminary age estimate (22.4 ± 0.3 Ma) much older than the Eagle Crag fission track date. An effort is now underway to date tuffs in the Anderson Ranch Formation by ID-TIMS zircon U-Pb geochronology to resolve this question.

Temnocyonine fossils referred to *Mammacyon* in the North American midcontinent lack proximity to tuffs but are associated with mammals that provide a biochronologic age. South Dakota *Mammacyon obtusidens* from the Porcupine Creek area occurs with early Arikareean mammals (*Miohippus*, *Desmatochoerus*, *Enhydrocyon*, *Nimravus*) that became extinct before the late Arikareean and do not occur in Harrison Formation faunas in western Nebraska. Faunas from southwestern South Dakota that include *Mammacyon obtusidens* are considered older than 25 Ma (Tedford et al., 2004).

Mammacyon ferocior from the Frick Laboratory's "north of Keeline" collecting area in southeast Wyoming is doubtless younger than *M. obtusidens* from South Dakota and is said to come from "Harrison" Formation rocks. However, the mammal fauna from north of Keeline does not include several of the most common Harrison Formation species (*Menoceras arikarense*, *Moropus elatus*, *Stenomylus hitchcocki*) from northwest Nebraska that occur in the stratotype of the formation at the head of Monroe Creek and also at Agate Fossil Beds National Monument. The small rhinoceros *Menoceras* and chalicothere *Moropus* are first occurrences in the Harrison Formation and are considered to be Asian immigrants. The absence of *Moropus* and *Menoceras* holds true for all Arikaree rocks termed "Harrison" by the Frick Laboratory collectors along the Wyoming Pine Ridge escarpment: these exposures extend from north of Keeline east nearly to the town of Van Tassell, a distance of ~38 mi (61 km). Additionally, the fauna from north of Keeline differs from the fauna of the Harrison Formation in northwest Nebraska in the presence of not only *Mammacyon ferocior*, a species unknown in Nebraska Harrison faunas, but also by the inclusion of a more primitive stenomyline camel (*Stenomylus keelinensis*), two rhinoceroses (*Diceratherium armatum* and *D. annectens*), the oreodont *Desmatochoerus*, and a small species of the equid *Kalobatippus* that precedes *K. agatensis* from the Harrison Formation at Agate. These mammals indicate an age for the Keeline "Harrison" fauna somewhat older than the mammal fauna from the stratotype Harrison Formation and the correlative Harrison sediments at Agate National Monument in Nebraska, dated by

←
sediments of the North American midcontinent indicative of semiarid to arid grassland and savanna. All fossils to common scale.

the 22.9 Ma Agate Ash. Thus, *Mammacyon ferocior*, the terminal species of its lineage, is considered here to be of latest Oligocene age, older than 23 Ma.

The age of *Mammacyon ferocior* and the "Harrison" beds north of Keeline (and their continuation eastward along the Wyoming Pine Ridge escarpment) can also be estimated from paleomagnetic sampling of the stratotype Monroe Creek–Harrison section in northwest Nebraska along Monroe Creek, north of the village of Harrison, and from a correlative section 5 mi (8 km) east at Pants Butte (MacFadden and Hunt, 1998; Hayes, 2004). The Keeline fauna seems to correspond stratigraphically to paleomagnetically calibrated sandstones termed the "upper Monroe Creek" beds (Peterson, 1907) that lie below the stratotype Harrison Formation of Hatcher (1902a) at the head of Monroe Creek. There the "upper Monroe Creek" beds comprise 240 ft of mostly unfossiliferous gray tuffaceous eolian sandstones (from 4640 to 4880 ft in elevation) that span approximately 3 million years from ~24.8 to 27.8 Ma. These beds appear to fall primarily within polarity chrons C9n, C8r, C8n, and C7Ar of the Global Polarity Time Scale (Hayes, 2004). *Mammacyon ferocior* and the "north of Keeline" fauna suggest a placement in the younger part of this interval due to affinity with the later-occurring Harrison fauna and the common occurrence of the oreodont *Promerycochoerus*.

The earliest evidence of *Delotrochanter* (CM 1603, *D. petersoni*) was collected in 1904 by O.A. Peterson from the Pine Ridge escarpment at the head of Warbonnet Creek in northwest Nebraska (Peterson, 1907). An identifiable gray tuffaceous sandstone adhering to these jaws allows them to be placed within an estimated stratigraphic interval of 200–300 ft in the upper part of the Pine Ridge Arikaree sequence. However, Peterson's (1907) attribution to the "upper Monroe Creek" horizon, and the field label indicating "middle Monroe Creek beds," does not permit assignment to a more limited stratigraphic level within these gray eolian sandstones. Nonetheless, *D. petersoni* is a much less advanced form in size and dentition than *D. oryktes* from the Harrison Formation, indicating a probable derivation from low in the "upper Monroe Creek" beds in Sioux County, possibly within or near polarity chron C8r. If correct, the first appearance of *Delotrochanter* conceivably could occur from ~26 to 27 Ma.

Sediments in the lower part of the Monroe Creek Canyon section along Monroe Creek, attributable to what Peterson (1907) would have termed "lower Monroe Creek" and "Gering" beds, show clear polarities correlating to chrons C9r and C10n (Hayes, 2004), establishing that this stratigraphic interval extends from 27.8 Ma to no older than 28.7 Ma (Gradstein et al., 2004). Rocks placed in chron C10n are anchored by an unpublished dated ash. The "lower Monroe Creek" beds at Wildcat Ridge in the southern Nebraska panhandle yielded an ash dated at ~27.8 Ma (Olson's Third Ash, Tedford et al., 1996: 316, 321), a date in agreement with polarity chrons inferred for the "lower Monroe Creek" beds at Pine Ridge.

Kew Quarry, California

The temnocyonine from Kew Quarry in the Sespe Formation of California is of particular interest since the fractured mandible (*Temnocyon* cf. *T. subferox*, LACM 470) is the only record of the subfamily in western North America outside the John Day region. LACM 470 and the rare remains from Florida show that temnocyonines likely occupied the southern United States from California to the Gulf and Atlantic coasts during the later Oligocene.

The age of the Kew Quarry fauna for some time has been considered problematic. Certain mammals are suggestive of a late Whitneyan, others of an early Arikareean age (Stock, 1932, 1933a, b, 1948; Wilson, 1949; Lander, 1983; Whistler and Lander, 2003; Tedford et al., 2004). Preference for the younger age of the Kew Quarry fauna is influenced largely by carnivores (*Temnocyon* cf. *T. subferox*, *Mesocyon brachyops*, *Eusmilus cerebralis*), the equid *Miohippus*, camel *Miotylopus gibbi*, and a cricetid rodent (?*Paciculus*), whereas a late Whitneyan age has been inferred from taxa occurring in the early Arikareean whose ranges extend into the Whitneyan: the rhinoceros *Subhyracodon*, nimravid *Nimravus brachyops*, canid *Ar-*

chaeocyon pavidus, anthracothere *Elomeryx armatus*, and hypertragulid *Hypertragulus calcaratus*.

Although a radioisotopic date for the quarry is not available, several carnivores from Kew Quarry were also found in the John Day Formation at Logan Butte, Oregon, where the beds are bracketed by the previously mentioned tuffs dating from 28.87 to 29.25 Ma. Thus, the Logan Butte fauna is apparently equivalent to the more northern John Day fauna occurring immediately below the Picture Gorge ignimbrite (28.7 Ma). Bryant (1996) thought fossils of *Eusmilus cerebralis* from Logan Butte and Kew Quarry were of early Arikareean age. Wang (1994: 57; Wang and Tedford, 2008) also regarded the holotype of *Mesocyon brachyops* from the butte and the sample of *M. brachyops* from Kew Quarry as early Arikareean. The *M. brachyops* holotype and the skull and partial skeleton of the plesiomorphic *Temnocyon altigenis* (UCMP 9999) were both found at UCMP locality 898 at Logan Butte. Thus, these carnivores date with some certainty between ~28.8 and 29.3 Ma, and collectively support an early Arikareean age. Of interest here is that *Temnocyon* cf. *T. subferox* (LACM 470) from Kew Quarry is not only a larger, more derived species than *T. altigenis* (UCMP 9999) from Logan Butte, but also relative to the entire *T. altigenis* sample from the John Day Formation. The presence of LACM 470 in the Kew Quarry fauna seems a particularly strong indicator of an early Arikareean age.

Some mammals from the quarry are mentioned as most compatible with a Whitneyan age. The nimravid mandible from Kew Quarry, assigned to *Nimravus brachyops* by Toohey (1959), was reported to be smaller than all John Day specimens of this species and closest in size to a *N. brachyops* mandible (UNSM 25491) from 2 ft above the upper Whitney ash (30.6 Ma, Prothero and Swisher, 1992) in western Nebraska. One of the largest John Day skulls of *N. brachyops* comes from UCMP locality 898 at Logan Butte: the Kew Quarry jaw and this skull are at the extremes of size for this species (possibly a small female and large male); both were regarded as conspecific and of early Arikareean age by Bryant (1996). The small rhinoceros, *Subhyracodon occidentalis*, considered a pre-Arikareean indicator based on its premolar dentition (Stock, 1933a; Lander, 1983), has been an influential taxon for those favoring a Whitneyan age (Lander, personal commun., 2002). Finally, the Kew Quarry equid *Miohippus*, also identified as a Whitneyan form, was considered by M.F. Skinner (personal commun., 1970) to be post-Whitneyan in age based on the crown height of m1 and twinned metastylid-metaconids of dp3–4 and m1.

Kew Quarry occurs in the upper member of the Sespe Formation in the Ventura Basin of southern California. Here a ~500 m composite section measured in the Las Posas Hills was mostly paleomagnetically reversed and initially correlated to either polarity chron C10r or C11r (Prothero et al., 1996) in the late early Oligocene. The upper member in the Santa Anna Mountains (~100 km southeast of the Las Posas Hills) was later correlated to chrons C10n-C10r (Calvano et al., 2003). More recent paleomagnetic and radioisotopic dating of the Sespe Formation in Los Angeles and Orange counties concluded that the regional episode of Oligocene Sespe deposition occurred from 28 to 30 Ma (Calvano et al., 2008: 58), with no Oligocene sediments older than 30 Ma, the lower boundary of the Arikareean NALMA. A Whitneyan age for Kew Quarry then seems unlikely. The current consensus accords the early Arikareean indicators priority and favors correlation to within chron C10r (Tedford et al., 2004), which extends from 28.7 to 29.4 Ma (Gradstein et al., 2004). The Whitneyan determinations apparently rest on preservation of relict taxa in the Kew Quarry fauna, a possibility initially noted by Stock (1932).

DISCUSSION AND CONCLUSIONS

Origin and Geographic Distribution of an Archaic Predator Guild

The continent-wide geographic distribution of temnocyonines from the Pacific Northwest to the central Great Plains and Florida suggests that the subfamily occupied a significant ecologic niche in North America for at least 7 million years from the late early

Oligocene to the early Miocene. Our knowledge of the group is primarily based upon the fossil record of two regions, the John Day basin of Oregon, where they were first discovered, and the central Great Plains of western Nebraska and eastern Wyoming. The John Day temnocyonines are radioisotopically documented from ~29 to 23.8 Ma; in the Great Plains, two lineages (*Temnocyon*, *Delotrochanter*) survive into the early Miocene.

Temnocyonine evolution is characterized by a progression from small (5–10 kg) to quite large (~65–80 kg) species and, simultaneously, involves a branching into both hypercarnivorous and durophagous lineages, defined by a singular dentition that allows the subfamily to be tracked over time. John Day temnocyonines differ sufficiently from Great Plains species to indicate a regional distinction, in accord with a long-recognized disparity between John Day and Great Plains faunas of Oligocene age (Tedford et al., 2004). The smaller carnivorous species, best represented in the John Day basin, were likely generalists with a rather catholic diet, whereas the large durophagous forms found in the Great Plains seem to be specialists responding to specific regional selection pressures.

Beginning with small fox-sized forms at the end of the early Oligocene, the subfamily evolved three principal lines, recognized in this study as genera (*Temnocyon*, *Mammacyon*, *Delotrochanter*). Temnocyonine diversity was established by the late Oligocene with the appearance of large hypercarnivorous (*Temnocyon ferox, T. fingeruti*) and durophagous (*Mammacyon obtusidens, M. ferocior*; *Delotrochanter petersoni*) species (fig. 70). Possibly extinct in the John Day basin by the end of the Oligocene, temnocyonines continued into the early Miocene in the Great Plains as four surviving species (*T. percussor*, *T. macrogenys*, *D. oryktes*, *D. major*).

Overall, the history of the Temnocyoninae appears to have been influenced by changes in the faunal dynamic of the time: (a) the absence of catlike predators (nimravids) after 25 Ma; (b) the absence of large bone-processing canids throughout the late Oligocene–early Miocene; (c) the development of semiarid to arid grassland ecosystems in the late Oligocene–Early Miocene; (d) the immigration of large Eurasian amphicyonine amphicyonids and hemicyonine ursids into North America accompanying a new climatic/tectonic regime unfolding during the early Miocene.

The dominant role of indigenous temnocyonines as predators during the late Oligocene–early Miocene interval in North America appears closely tied to the increase in body size in the various lineages. This increase is apparently linked to the opening of previously occupied niches as less-adapted species declined to extinction. Prior to the appearance of large temnocyonines, the hypercarnivorous niche in the Oligocene belonged to nimravid cats (Bryant, 1991, 1996; Martin, 1998), and the niche for processing hard food materials to durophagous hesperocyonine canids (*Enhydrocyon*, *Philotrox*; Wang, 1994), essentially small "hyaenoid" dogs. When most species in these groups become extinct in the late Oligocene, temnocyonines begin to diversify. By the early Miocene, nimravids and bone-crushing hesperocyonines are gone, replaced by large species of *Temnocyon* and *Delotrochanter*. True cats and hyaenids were late arrivals in North America, the first felids migrating into North America from Eurasia at ~16.5–17 Ma at the end of the early Miocene, and a hyaenid not appearing until the Pliocene.

Temnocyonines have not been identified outside of North America. However, European paleontologists (Viret, 1929; Bonis, 1973) have noted a pronounced dental similarity between temnocyonines and late Oligocene-early Miocene European haplocyonine amphicyonids. The two groups apparently evolved in parallel from a common Eocene or early Oligocene amphicyonid ancestry, each becoming geographically isolated, the haplocyonines in Europe and temnocyonines in North America. Neither group is certainly identified in Asia. The tall premolars (p2–4, P2–3) and specialized crushing cheek teeth (p4-m2, P4–M1) shared by the two subfamilies comprise the principal evidence for relationship. Late Oligocene and early Miocene temnocyonines evolved the most highly developed crushing dentitions, which are not found among haplocyonines: *Haplocyonopsis crassidens* (Bonis, 1973) and

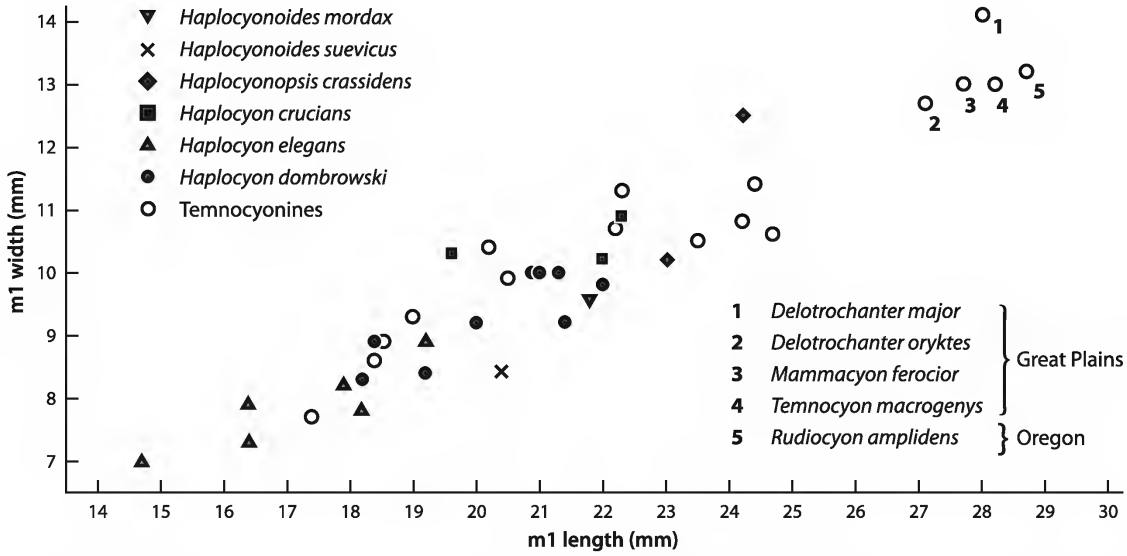


Fig. 71. Dimensions of m1 for species of North American temnocyonine and European haplocyonine amphicyonids as an indication of body size. The largest of these carnivores are durophagous temnocyonines (#1-5) occupying grassland-savannas of the Great Plains and Oregon.

Haplocyonoides mordax and *Hcyd. suevicus* (Hürzeler, 1940; Peigné and Heizmann, 2003) make the closest approach.

The proportions of M1 and P4 (A/B, C/D ratios, table 6) best illustrate the more pronounced crushing adaptations of these teeth in *Mammacyon* and *Delotrochanter* relative to haplocyonines. Haplocyonines show a progressive development of a modest crushing P4 (C/D ratios: *Haplocyon elegans*, 1.54–1.59; *H. dombrowski*, 1.45–1.46; *H. crucians*, 1.32; *Haplocyonoides suevicus*, ~1.35; *Haplocyonoides mordax*, 1.23–1.26, *Haplocyonopsis crassidens*, 1.27), yet they fail to develop the particularly robust P4 proportions and large crushing protocones of *Mammacyon* and *Delotrochanter* species (C/D ratios, 1.13–1.27). Similarly, the lingual expansion of M1 to form a crushing platform in haplocyonines (A/B ratios: ~1.42–1.63) approximates the grade of M1 development found in species of *Temnocyon* (1.44–1.66) but does not result in the massive M1 crushing platforms of *Mammacyon* and *Delotrochanter* reflected in their A/B ratios (1.12–1.36). Dimensions of the lower carnassial, plotted as a proxy for body size for all species of the two subfamilies (fig. 71), show that the largest of these carnivorans were North American: the terminal durophagous species of *Mammacyon* and *Delotrochanter*, the huge *Temnocyon macrogenys*, and the John Day *Rudiocyon amplidens*.

Global Climate and the Temnocyonine Radiation

The temnocyonine radiation in North America immediately followed a marked climatic transition from the warmer, more equable world of the Eocene to the cooler, more seasonal climates of the Oligocene. Once the subfamily is established, species were subjected to an interval of much warmer climate during the late Oligocene. Global deep-sea oxygen isotope records orbitally tuned to the Global Polarity Time Scale (GPTS, Zachos et al., 2001, 2008; Billups et al., 2004; Francis et al., 2009) provide a temporal context for evaluation of the climate during temnocyonine diversification (fig. 72).

The cooler climate of the Oligocene, prefaced by the Oi-1 glaciation of Antarctica at ~34 Ma, preceded the first appearance of temnocyonines between 29 and 30 Ma. The principal temnocyonine lineages must have been established during the relatively stable climate of the earlier Oligocene from ~33 Ma to 26.8 Ma. Species of *Temnocyon* and

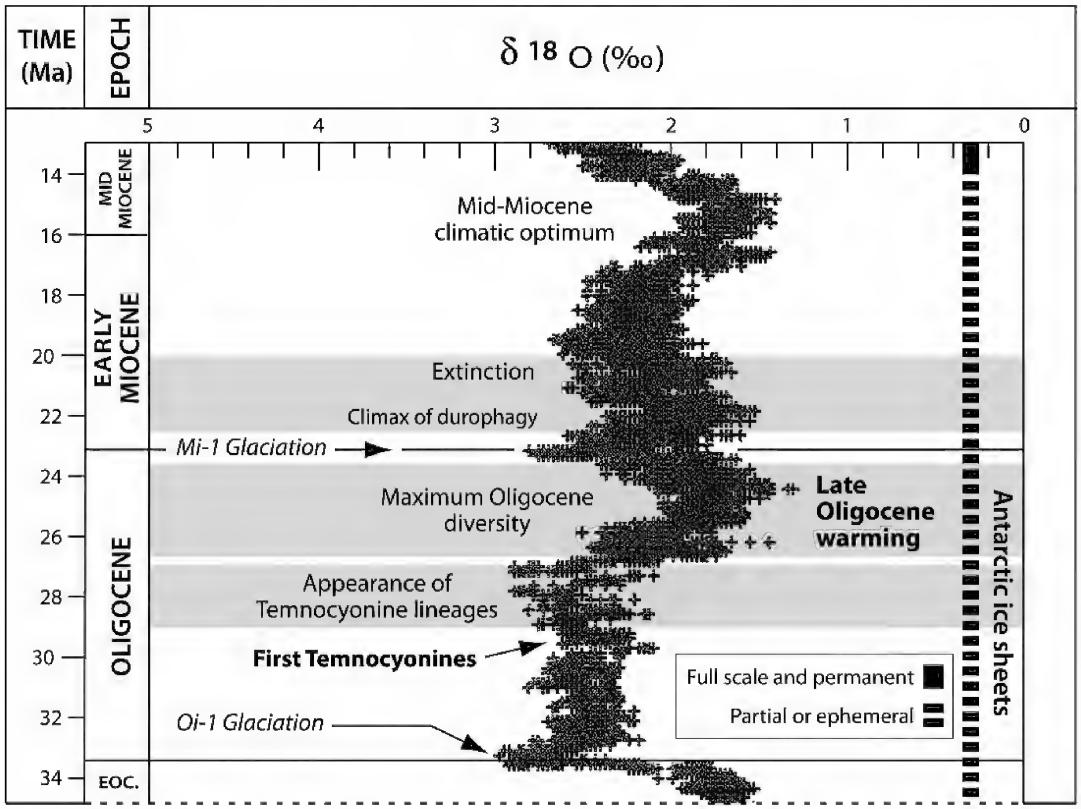


Fig. 72. Orbitally tuned Oligocene-Miocene global oxygen isotope record (after Zachos et al., 2008; Francis et al., 2009) relative to the appearance and radiation of North American temnocyonine amphicyonids.

Mammacyon first appear in this interval, as does *Rudiocyon amplidens* and the earliest species of *Delotrochanter*. From ~26.8 Ma to immediately prior to the end of the Oligocene at 23 Ma, temnocyonines achieved their maximum diversity. A size increase in *Temnocyon* and *Mammacyon* occurred at this time, and likely included *Delotrochanter*. Of interest is that temnocyonine diversification coincides with the Late Oligocene Warming (LOW) event, an accelerated warming trend beginning at ~26.8 Ma that reached a maximum at ~25–24 Ma, and then declined until the global cooling that accompanied the Mi-1 glaciation at 23 Ma, the Oligocene-Miocene (O/M) boundary (Francis et al., 2009; Zachos et al., 2008).

The climax of the LOW, occurring between ~25 and 24 Ma, may have attained a regional warmth equivalent to that achieved in the late Eocene (fig. 72). This interval is difficult to discern with precision in terrestrial sediments, both in Oregon and the Great Plains, due to the scarcity of reliably dated tuffs or ash-flows of that age. However, in the midcontinent, the overall sedimentary record indicates that this was a stable, warm period characterized by an arid to semiarid seasonal climate. Species of *Temnocyon* and *Delotrochanter* apparently were increasing in size at this time since large species of both of these genera appear at ~23 Ma in the early Miocene.

The warmth of the late Oligocene yielded abruptly to an acute cold interval at the O/M boundary at 23 Ma (Billups et al., 2004; Zachos et al., 2008; Francis et al., 2009). In the midcontinent, emerging grasslands may have been favored by this cooler episode. By the late Oligocene there is evidence of the spread of expansive grasslands and open woodlands, later transitioning to savanna with riparian elements in the early Miocene (Stromberg, 2004).

Temnocyonines (*Temnocyon percussor*, *T. macrogenys*; *Delotrochanter oryktes*, *D. major*) at the dawn of the Neogene are large durophagous carnivores. They were joined by immigrant carnivores and ungulates that appear in North America at the time of the Mi-1 glacial event at ~23 Ma (Webb and Updyke, 1995; Tedford et al., 2004). These temnocyonines from the Harrison and Anderson Ranch formations represent the climax of the radiation, and persist into the latest Arikareean (Ar4), where the formidable *Temnocyon macrogenys* and *Delotrochanter major* are the last of the subfamily.

Following the Mi-1 glacial episode, a warmer climate returned in the early Miocene and continued to the mid-Miocene climatic optimum, an 8 million-year interval characterized by abundant and diversified ungulate and carnivorous mammals adapted to open terrain and the spread of regional grasslands and savanna. Global ice volume remained, but was much reduced (Zachos et al., 2001). However, by the beginning of the Hemingfordian NALMA (~18.5–18.8 Ma), temnocyonines are no longer evident as members of the predator guild.

Regional Climate and Temnocyonine Diversity

Recent investigations in biochronology, stratigraphy, sedimentology, and taphonomy of the John Day region and the central Great Plains (western Nebraska–southeast Wyoming) contribute to a more nuanced picture of the temnocyonine radiation relative to the climate and faunal dynamic in these areas.

In the Pacific Northwest, a warm climate in the late Eocene supported humid, forested habitats in the John Day basin. Based on paleosol analysis (Retallack, 1997, 2007), the early Oligocene to the early late Oligocene (30–27 Ma) saw a continuation of generally warm and wet conditions in the region. Significant woodlands occur as late as 30 Ma, then decline to 27 Ma, as grassland expanded. Predominantly bunch grassland and sagebrush steppe is reported in central Oregon, appearing at 27 Ma (Retallack, 2007). A second expansion of grassland in the late Oligocene (25–24 Ma) is thought to have accompanied a decline in sagebrush. The terminal Oligocene is seen as unusually cool and dry, possibly influenced by the rain shadow created by the ancestral Cascades. However, wooded stream courses must have been present in the terminal Oligocene and early Miocene, as evidenced by fossil wood common in stream channel sediments after ~24 Ma (Hunt and Stepleton, 2004). The drying trend of the Oligocene culminated in cooler, semiarid, open grasslands with riparian woodland and possible savanna in the early Miocene. Paleosol sequences interpreted as evidence of Milankovitch cyclicity are said to indicate periodic climatic oscillation (Retallack et al., 2004).

In the central Great Plains east of the Rocky Mountains, there is substantial evidence that a continental climate prevailed during the late Oligocene and early Miocene at the time of temnocyonine diversification (Stanley, 1976; Stanley and Benson, 1979; Vicars and Breyer, 1981; Swinehart et al., 1985; Hunt, 1978, 1985, 1990). The Arikaree Group is represented by a vast expanse of eolian sediment, distributed over a terrain of extremely low relief, incised by shallow, broad paleovalleys of the braided-channel, distributary type. Arikaree lithofacies are the residuum of dryland environments transected by ephemeral drainages bordered by dunes, dikaka, grassland, and savanna. Fluvial bedforms indicate stream energies consonant with rare, episodic floods, interrupting prolonged intervals of nondeposition or brief eolian influx. Interchannel reaches made up of loessic, wind-blown fine sand and silt, are devoid of evidence of vegetation other than grasses and other low-growing plants. Fossil wood is rare and only occasionally found in fluvial deposits; paleosols are immature, and dune bedforms are common. Shallow ephemeral lakes and waterholes are the only standing bodies of water and share a depauperate biota of pulmonate gastropods, ostracods, charophyte algae, and diatoms. Evidence of aquatic vertebrates is infrequent. In the early Miocene, fossils of water-dependent mammals (notably chalicotheres and rhinoceros) are concentrated in waterholes and in stream channels, whereas the common species of the interfluves are camels and oreodonts, which appear to tolerate dry

conditions. Enduring catastrophic droughts are evidenced by several mass death events.

This setting would impose a daunting series of demands upon medium- to large-sized carnivores. Perhaps most relevant is the lack of vegetative cover, requiring the search and pursuit of prey in the open, and over long distances. The necessity of concealing, protecting, and feeding pups in an open, arid landscape, while hunting at a great distance from them, no doubt led to denning behaviors and perhaps (but not necessarily) to pack formation. Cooperative hunting is reported as essential for lions in the plains of Namibia during the dry season, a time of environmental stress (Stander, 1992a, b). More assuredly, durophagy would improve reproductive success by enabling adults to rapidly process meat and bone, thereby adding an important nutrient source (bone and bone marrow) to the diet, and also perhaps (but again, not certainly) adding regurgitative food transfer to the repertoire of pup rearing strategies. Van Valkenburgh (1989) noted that carnivores utilizing bone are likely to prosper in settings such as the plains of the Serengeti where carcasses become seasonally available, an environment comparable to the central Great Plains in the early Miocene.

The only competitors for a durophagous role during the Oligocene and early Miocene are large entelodont artiodactyls (Joeckel, 1990; Hunt and Tedford, 1993; Hunt, 2004). Entelodonts are much larger than temnocyonines, suggesting a partitioning of the food resource since the largest herbivores (chalicotheres and several large rhinoceroses) would supply carcasses that entelodonts could utilize more easily than even the largest temnocyonines. The temnocyonine-entelodont association (Hunt and Tedford, 1993) is thought to be important for durophagous processing of carcasses in open dryland environments of the Great Plains during the late Oligocene–earliest Miocene in North America.

The large, cursorial, crushing-toothed species of *Mammacyon* and *Delotrochanter* seem a direct response to the development of open, semiarid to arid grassland environments found in the North American midcontinent at the end of the Oligocene and continuing into the early Miocene. In these grasslands east of the Rocky Mountain uplifts, ungulate biomass would be expected to contribute both active prey and a steady supply of carcasses over time, as it does in the present East African savannas. The crushing dentitions and cursorial limbs of the large temnocyonines appear to be adaptations to these environments. A cursorial striding gait allows travel over a large territory, and robust skulls and teeth were well suited for both active carnivory and grinding of hard material such as bone.

Epilogue: Cursorial Predators and Durophagy

Durophagous cursorial temnocyonines existed in the Great Plains for about 5 million years from ~27 Ma to at least 22 Ma. An explanation for the scarcity of these large durophagous temnocyonines in the John Day Formation is not readily apparent: perhaps it is simply the random, haphazard nature of fossil preservation or even the result of numerically small and declining populations. However, based on the present fossil record, the youngest John Day species are not as specialized for durophagy as those in the Great Plains, and no John Day skeletons attain the advanced cursorial limbs seen in the temnocyonines from the Great Plains. *Temnocyon fingeruti*, dated at ~23.8 Ma, is a large hypercarnivore, with a wolflike dentition, and is of latest Oligocene age. Cursorial limbs seem likely but remain undocumented.

No early Miocene temnocyonines have been found in the John Day basin. A few rare John Day fossils, such as the Haystack Valley *Mammacyon* maxilla (LACM 5386) and the jaw fragment of *Rudiocyon* (LACM 480), indicate the existence of durophagous species, but these are probably early late Oligocene (>27 Ma) in age; hence they precede the large durophagous Great Plains species of the late Oligocene and early Miocene. The small postcarnassial molars of *Rudiocyon* are less developed than the equivalent crushing teeth in the Great Plains species, and suggest a more diverse diet.

Active hunting of large prey seems within the capability of the large cursorial temnocyonines. That large durophagous temnocyonines were exclusively scavengers seems

unlikely. Spotted hyenas (*Crocuta crocuta*), while scavengers, are also capable hunters. Similarly, most large carnivores scavenge when carrion is available. Living carnivores that hunt large prey have broad muzzles, large, strong incisor and canine teeth, and deep jaws that come into play when encountering the stresses of grasping and holding a large animal (Van Valkenburgh and Ruff, 1987; Van Valkenburgh and Koepfli, 1993). Dependance on skull and jaws during a kill derives from an inability to use a cursorially adapted forelimb for prey capture and retention. *Mammacyon* and *Delotrochanter* have forelimbs similar to those of the wolf, ill-adapted for grasping; however, they do have robust skulls, broad snouts with large canines and incisors, strong mandibular symphyses, and deep mandibles that far exceed jaw depth in the living pack-hunting canids. The prominent premolar battery of temnocyonines is doubtless an added advantage in grasping and holding prey, and the carnassials and crushing molars contribute a complementary ability to utilize both meat and bone in the diet. These beardogs likely combined active hunting with scavenging. Some temnocyonines (*Delotrochanter oryktes*, *D. major*) could be termed hyaenid ecomorphs based on skull form and crushing cheek teeth, whereas others (*Temnocyon fingeruti*, *T. ferox*) parallel the large living canids in their skull and dentition, with several of the larger species (*Mammacyon ferocior*, *M. obtusidens*, *Delotrochanter oryktes*) tending toward a cursorial capability reminiscent of living wolves.

Temnocyonines are extinct by the end of the Arikareean NALMA. They share the late/latest Arikareean interval (Ar3, Ar4) with daphoenine beardogs (Hunt, 2002b) and the amphicyonine *Ysengrinia* (Hunt, 2002a). In the early Hemingfordian, temnocyonines are replaced by amphicyonines (*Amphicyon*, *Cynelos*), a large cursorial daphoenine (*Borocyon*), and hemicyonine ursids. Amphicyonines and hemicyonines first appear in North America in the late Arikareean as Eurasian immigrants and become the dominant predators of the later Hemingfordian, living together at that time with mid-sized felids and canids. The Arikareean-Hemingfordian faunal turnover, both in the Great Plains and Pacific Northwest, involves a dramatic change in the large carnivore guild in North America.

As temnocyonine lineages increased in body size in parallel during the late Oligocene and early Miocene, becoming dentally specialized for divergent ecologic roles, their decline to extinction conforms to an iterative pattern common to large Cenozoic hypercarnivores (Van Valkenburgh, 2007): the vulnerability of small populations isolated at high trophic levels to extreme environmental stress, here likely the result of the documented climatic instability occurring during the Paleogene-Neogene transition in North America and to competition from immigrant Eurasian carnivores.

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The skull of *T. fingeruti* was found and collected by M. Fingerut and G. Pierson

along Balm Creek, east of Haystack Valley, in the John Day Formation. The discovery of the skull initiated our lithostratigraphic/biochronologic research on the upper John Day beds in the Kimberly-Haystack Valley region (Hunt and Stepleton, 2004, 2006). It was loaned for preparation and description to UNSM by M. Fingerut and D. Taylor at Portland State University, Portland, Oregon. T. Fremd, John Day Fossil Beds National Monument, Oregon, provided an introduction to temnocyonine localities in the John Day Formation and helpful collaboration over many years. The National Park Service (NPS) at Agate National Monument permitted excavation of the carnivore dens at Beardog Hill where UNSM discovered the skull and foot elements of *Delotrochanter oryktes*. Research at the national monument received the constant support and cooperation of rangers and staff: D. Buckley, M. Hertig, B. and D. Mack, L. Mansfield, W. Matthews, R. Miller, W. Taylor, R. Todd, A. Wilson, and superintendents A.J. Banta, J. Hill, R. Knudson, J. Kyral, J. Rapier, L. Reed, B. Stransky, and R. Weaver. Midwest Regional Chief of Interpretation (NPS) T. Richter has been an enthusiastic advocate and participant in all Agate research.

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APPENDIX 1

Minimum Number of Individuals (MNI) of Temnocyoninae in North American Collections

Taxon	N	Museum No.
Temnocyon altigenis	6	(AMNH 6855-6857, USNM 7940, UCMP 1549, 9999)
Temnocyon subferox	1	(YPM 10065)
Temnocyon cf. *T. subferox*	1	(LACM 470)
Temnocyon fingeruti	1	(NM 280/61)
Temnocyon ferox	1	(YPM-PU 10787)
Temnocyon percussor	3	(AMNH 81005, 81054, 81047)
Temnocyon macrogenys	1	(F:AM 54139)
Rudiocyon amplidens	1	(LACM 480)
Mammacyon obtusidens	3	(ACM 34-41, LACM 9194, 5386)
Mammacyon ferocior	2	(F:AM 27562, 54134)
cf. *Mammacyon*	1	(LACM 15908)
Delotrochanter petersoni	1	(CM 1603)
Delotrochanter oryktes	4	(ACM 4804, 4804A, UNSM 47800, YPM 24872)
Delotrochanter major	1	(F:AM 27561)
Temnocyoninae indet.	2	(UF 16908, 24203)
	1	(TRO 386-388, 390, 661)
Total MNI	30	

APPENDIX 2

Measurement of Temnocyonine Mandibles (in mm) and Derived Log_{10} Values

Taxon	Mus. no.	DL[a]	LAP[a]	LAM[a]	D_yP	D_xP	D_yM	D_xM
T. altigenis	UCMP 9999	136	79	62	21.5	10.0	23.3	9.2
T. ferox	YPM-PU 10787	195	110	88	37.3	15.7	39.6	14.5
T. fingeruti	NM 280/61	200	112	89	32.8	12	34.5	12–13
T. macrogenys	F:AM 54139	254	143	115	53.5	15.2	53.0	14.2
M. obtusidens	LACM 9194	188	107	84	32.9	15.1	38	14.5
D. oryktes	ACM 4804	202	119	90	39.1	14.6	45.6	14.0
T. altigenis	UCMP 9999	2.13	1.90	1.79	1.33	1.00	1.37	0.96
T. ferox	YPM-PU 10787	2.29	2.04	1.94	1.57	1.20	1.60	1.16
T. fingeruti	NM 280/61	2.30	2.05	1.95	1.52	1.08	1.54	1.08
T. macrogenys	F:AM 54139	2.40	2.15	2.06	1.73	1.20	1.72	1.15
M. obtusidens	LACM 9194	2.27	2.03	1.92	1.52	1.18	1.58	1.16
D. oryktes	ACM 4804	2.31	2.08	1.95	1.59	1.16	1.66	1.15

[a]DL, LAP, and LAM measurements are estimated because the ascending ramus and articular condyle are missing in all mandibles except for those of *T. macrogenys* and *D. oryktes*, which are intact.

Abbreviations: DL, dentary length; LA, working side lever arm length; D_y, mandibular depth; D_x, mandibular width; P, measured at interdental gap between p4 and m1; M, measured at interdental gap between m1 and m2.

APPENDIX 3

Calculations from Mandibular Measurements (in cm): Section Moduli (Zx, Zy), Working Side Lever Arm (L), Parasagittal and Transverse Bending Strength (Zx/L, Zy/L), and Relative Magnitude of Bending Resistance (Zx/Zy) at Various Loci along the Mandibular Corpus[a]

	canine	p3p4	p4m1	m1m2	m2m3	post m3	dentary length (cm)
Temnocyon macrogenys							
Zx	5.97	2.65	3.20	3.92	5.03	5.70	25.4
Zy	4.57	0.82	1.20	1.05	1.24	1.31	
L	22.60	16.69	14.30	11.50	9.72	8.77	
log Zx/L	−0.58	−0.80	−0.65	−0.46	−0.28	−0.19	
log Zy/L	−0.69	−1.30	−1.07	−1.05	−0.89	−0.83	
Zx/Zy	1.30	3.23	2.66	3.73	4.05	4.35	
Canis lupus							
Zx	2.00	1.32	1.82	1.79	1.83	2.00	19.13
Zy	2.22	0.68	0.86	0.67	0.59	0.62	
L	16.73	12.28	10.62	7.90	6.56	5.95	
log Zx/L	−0.92	−0.97	−0.77	−0.64	−0.55	−0.47	
log Zy/L	−0.87	−1.25	−1.09	−1.07	−1.05	−0.98	
Zx/Zy	0.90	1.94	2.12	2.67	3.10	3.23	
Borocyon robustum							
Zx	6.07	3.61	4.23	5.71	5.87	7.22	24.0
Zy	5.06	1.62	1.75	2.22	2.04	2.17	
L	21.80	16.90	14.80	11.54	9.57	8.50	
log Zx/L	−0.55	−0.67	−0.54	−0.31	−0.21	−0.07	
log Zy/L	−0.63	−1.02	−0.93	−0.71	−0.67	−0.59	
Zx/Zy	1.20	2.23	2.41	2.56	2.88	3.33	
Delotrochanter oryktes							
Zx	5.12	1.97	2.19	2.88	3.57	3.61	20.2
Zy	3.50	0.63	0.82	0.89	0.89	0.80	
L	18.10	13.80	11.81	9.00	7.73	6.90	
log Zx/L	−0.55	−0.85	−0.73	−0.49	−0.34	−0.28	
log Zy/L	−0.71	−1.34	−1.16	−1.00	−0.94	−0.94	
Zx/Zy	1.46	3.13	2.67	3.24	4.01	4.51	

	canine	p3p4	p4m1	post m1	
Crocuta crocuta					
Zx	3.79	2.31	3.06	3.40	17.50
Zy	3.16	1.20	1.29	0.99	
L	15.47	10.85	8.67	5.76	
log Zx/L	−0.61	−0.67	−0.45	−0.23	
log Zy/L	−0.69	−0.95	−0.83	−0.76	
Zx/Zy	1.20	1.92	2.37	3.43	
Panthera leo					
Zx	8.21	3.58	4.35	5.17	22.95
Zy	6.58	1.85	2.06	2.27	
L	19.79	15.61	12.98	9.97	
log Zx/L	−0.38	−0.64	−0.47	−0.28	
log Zy/L	−0.48	−0.93	−0.80	−0.64	
Zx/Zy	1.25	1.94	2.11	2.28	

[a]Data for *Canis lupus, Crocuta crocuta*, and *Panthera leo* are from Therrien (2005) and represent sample means for these species. Data for the amphicyonids (*Temnocyon macrogenys, Delotrochanter oryktes, Borocyon robustum*) were calculated from single mandibles.